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MAATALOUS-METSÄTIETEELLINEN TIEDEKUNTA

Variability and Mixed-Severity Disturbances Characterize Unmanaged Southern Boreal Forests in Russian Karelia

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Tiivistelmä – Abstrakt – Abstract

Increasing human impact has radically changed the forest structure and depleted the area of natural forests in many regions. In spite of active natural forest research during the last decades, the current knowledge on the southern boreal region, deciduous and mixed forests fall short. The knowledge on natural forests can be utilized for planning sustainable forestry, conservation measures or in environmental impact assessments regarding human influence on forests. The natural disturbance dynamics can be used as a model in silviculture, for example in the planning of restoration activities or commercial forest cuttings. The underlying presumption is that emulating natural forest dynamics can help to preserve such values as the forest biodiversity or resilience.

In this study we, investigated the historical variability of disturbances in four different sites in southern boreal forests of Russian Karelia. The target was to determine the disturbance frequency, intensity and range in different spatial scales (plot, site/stand, regional). Also the connection between disturbance quality and forest characteristics was explored.

To gather field data and extract increment cores from canopy trees, we established altogether 14 sample plots in four different sites (3-5 per site). We used standard dendroecological methods to record growth releases and gap recruitment from individual trees, indicating past disturbance. With this information, we reconstructed the disturbance chronologies for all plots and sites from the past two or three centuries.

From the studied forest sites, two were spruce-dominated stands and one pine-dominated stand. One stand represented mixed-forests with quite an even mix of pine, larch, spruce, and birch trees. The age structure of the forests was uneven-aged in three of the sites. As an exception was the pine-dominated site with relatively even-aged trees (80-100 years). The disturbance chronologies showed significant variation in spatial and temporal scales between sites and sample plots. During the last three centuries (22-26 decades of observation), all the sites had low (0-20%) to moderate (20-40%) or low to high severity (>40%) disturbances. All the sites had gone through a stand-scale disturbance, but no evidence on regional scale disturbance was found. There was no clear connection between forest characteristics and disturbance quality, albeit the data was too small to detect any strong interdependence.

The disturbance dynamics showed remarkable variability in disturbance frequency, intensity, and range. The results emphasize the natural heterogeneity and variance related to forest structure, composition and disturbance history. These results back up the prior understanding of the disturbance regime in the Karelian region.

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disturbance dynamics, dendrochronology, disturbance history, dendrochronology

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Tiivistelmä – Abstrakt – Abstract

Kasvava ihmistoiminta on vähentänyt luonnonmetsien määrää radikaalisti viimeisten vuosikymmenten aikana. Vaikka luonnonmetsiä on tutkittu aktiivisesti 1990-luvulta alkaen, tutkimustiedossa on vielä paljon puutteita, erityisesti eteläboreaalisten metsien ja lehti- ja sekametsien osalta. Luonnonmetsätutkimuksesta saatua tietoa voidaan hyödyntää esimerkiksi vertailukohtana ihmisen toiminnan vaikutuksia arvioitaessa tai kestävän metsätalouden suunnittelussa. Luontaista häiriödynamiikkaa voidaan käyttää mallina metsänhoidossa, esimerkiksi ennallistamisen tai talousmetsien hoitotoimenpiteiden suunnittelussa. Taustalla on tällöin oletus, että luontainen häiriödynamiikka (tai sen emulointi) auttaa säilyttämään paremmin sellaisia metsän ominaisuuksia tai arvoja, kuten biodiversiteetti ja resilienssi.

Tämän tutkimuksen tarkoituksena oli selvittää häiriöiden historiallista vaihtelua ja vaikutusta metsän rakenteeseen neljällä eteläboreaalisen metsän kohteella Venäjän Karjalassa. Tavoitteena oli määrittää häiriöiden voimakkuus (intensiteetti), frekvenssi ja alueellinen mittakaava. Lisäksi tarkasteltiin mahdollista yhteyttä häiriöiden laadun ja metsän ominaisuuksien (metsätyypin ja puulajien) välillä.

Neljälle tutkimuskohteelle perustettiin yhteensä 14 koealaa, joilta mitattiin puustotunnukset ja kairattiin lustonäytteet yhteensä 140:stä koepuusta. Lustonäytteet analysoitiin dendroekologisin menetelmin. Häiriöitä ilmentävistä, latvuskerrokseen päässeistä (vapautuneista) ja aukkoon syntyneistä puista muodostettiin häiriökronologiat kohteille ja koealoille.

Tutkituista kohteista kaksi oli kuusivaltaisia, yksi mäntyvaltainen ja yksi sekametsä. Kolme kohteista oli eri-ikäisrakenteisia ja männikkö oli melko tasaikäinen (80-100v). Häiriöissä esiintyi suurta ajallista ja alueellista vaihtelua kohteiden ja koealojen välillä. Kaikilla kohteilla esiintyi viimeisten kahden tai kolmen vuosisadan aikana voimakkuudeltaan vaihtelevia häiriöitä matalasta (0-20%) keskisuureen (20-40%) tai matalasta suureen (>40%). Kaikilla kohteilla esiintyi metsikkötason häiriöitä, mutta todisteita alueellisen tason häiriöistä ei löytynyt. Metsän ominaisuuksien ja häiriöiden laadun välillä ei havaittu selvää yhteyttä.

Häiriödynamiikoissa esiintyi huomattavaa vaihtelua frekvenssin, intensiteetin ja vaihteluvälin suhteen. Tulokset korostavat metsien rakenteen ja häiriöhistorian luonnollista vaihtelua. Tulokset tukevat aiempaa häiriötutkimusta Venäjän Karjalasta ja antavat arvokasta lisätietoa eteläboreaalisten metsien häiriödynamiikasta.

Avainsanat – Nyckelord – Keywords
häiriödynamiikka, dendrokronologia, häiriökronologia, dendroekologia, luonnonmetsä

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Table of Contents

1 INTRODUCTION

The boreal coniferous forest zone extends around the whole northern hemisphere and covers over 14 million km^2 (Shorohova et al. 2009). It maintains a large number of ecosystems and habitats, offers vital ecosystem services, like hydrologic and climate regulation, and has a significant role in the conservation of biodiversity. Increasing human impact has radically changed the forest structure and depleted the area of natural forests in many regions (Kuuluvainen et al. 2004, Shorohova et al. 2009). For example, in the Fennoscandian region, despite the vast forest resources, only a small fraction of the forest cover is in natural or near natural state (Horne et al. 2006, Kuuluvainen et al. 2004).

1.1 Why natural forest research matters

The first notable scientific research regarding natural forests in the Fennoscandian region was published in the early 20th century. At the time, there was still plenty of relatively vast forests outside of major human impact, suitable for ecological research (Kuuluvainen & Aakala 2011). For many decades, there was little interest in the natural forest research until the beginning of the 1990s. Therefore, most of the research related to natural boreal forests has been made in recent decades (Kuuluvainen & Aakala 2011). A major challenge for exploration has been the rapid loss of natural forests due to human activity and intense forestry after the World War II. At the present, only 1.5% of forest cover in southern Finland remain in protected areas outside of commercial forestry (Horne et al. 2006). Most of the natural forest areas are small, isolated fragments that cannot support the original taxa or disturbance dynamics which makes it impossible to establish sufficient research frame for natural disturbance dynamics. Especially, current knowledge on the southern boreal region, deciduous and mixed forests fall short (Kuuluvainen & Aakala 2011).

Research on natural forests provides understanding of the structure, dynamics and ecology of the natural forest ecosystem. This knowledge can be utilized for planning sustainable forestry, conservation measures or in environmental impact assessments

regarding human influence on forests (Lindenmayer & Franklin 2002, pp. 55-56, Kuuluvainen & Grenfell 2012). Natural disturbance dynamics can be used as a model in silviculture, for example in the planning of restoration activities or commercial forest cuttings (Landres et al. 1999). The underlying presumption or hypothesis is that emulating natural forest dynamics can help preserve values such as forest biodiversity or resilience (Drever et al. 2006, Kuuluvainen & Grenfell 2012).

Emulation of natural disturbances in forestry has been a major paradigm shift in the North American silviculture and forest sciences (Gauthier & Vaillancourt 2009 p. 17, Long 2009, Stockdale et al. 2016) and is gradually gaining ground in Finnish forestry institutions (Kilpinen 2016). Using natural disturbances as a model requires careful consideration of the natural reference state (including natural range of variability and disturbance regimes) for which the management aims at. Ideally, the reference can be derived from local, natural forest research but in most cases this is not possible. As a secondary information source, studies from similar areas/conditions, historical reconstructions based on dendrochronology, fire scars, and historical land use data, can be utilized (Kuuluvainen et al. 2004 p. 69, Stockdale et al. 2016). In addition, simulation models provide helpful stand and landscape scale information to some extent. For example, the average age distribution of stands in a forested region can be estimated from knowledge on disturbance regimes and from proportion and quality of disturbances (Pennanen 2002, Pennanen & Kuuluvainen 2002).

1.2 Disturbance dynamics in boreal forests

The structure and composition of natural forests are continuously shaped by disturbances and following successions. Disturbances, like forest fires or storms, can be defined as rapid, destructive change (causing tree mortality) and successions as long-lasting, constructing progression (White & Pickett 1985). Disturbances and the following successions are part of the natural, dynamic ecosystem and have an important role in maintaining the natural forest structure, biodiversity and resilience (Kuuluvainen et al. 2004 p.49, Drever et al. 2006). The quality, frequency, intensity, and range of disturbances vary greatly in different landscape scales, and together with various succession paths, they make the forest a heterogeneous and diverse environment.

Based on earlier research, boreal forests can be roughly divided into three different categories of disturbance dynamics and corresponding disturbance regimes (Angelstam & Kuuluvainen 2004, Kuuluvainen & Aakala 2011). The categories of disturbance dynamics are 1) succession after intensive, stand-replacing disturbance, 2) cohort dynamics after partially replacing disturbance and 3) gap dynamics when a single tree or group of trees die. Disturbance regime means the disturbance or combination of disturbances that typically occur in a certain landscape over extended time. The regimes are characterized by the frequency, severity and areal extent of disturbances (Kneeshaw et al. 2011). In the first category, the disturbances usually consist of intense forest fires or wind storms (allogenic disturbances), in which almost all the trees die. The cohort structures can be caused for instance, by surface fires or exceptionally harsh weather conditions that kill one age or size group of saplings or trees. The gap dynamics is usually due to internal (autogenic) insect and fungi caused die back.

The disturbance regimes in boreal Fennoscandia and western Russia are characterized by mosaic of forests, peatlands, lakes, and the semi-maritime climate that create diversity in landscape conditions. In an exhaustive review article on circumboreal forests, Kneeshaw et al. (2011) estimated the prevalence of different disturbance types based on fire cycles and occurrence. They suggest that in Fennoscandia, the maritime and northern, humid climate favors gap dynamics (in Norway, Sweden, northern Finland) and in the more continental areas (middle parts of Finland, Russian Karelia) surface fires prevail. However, these areas have long tradition of human use which makes it difficult to define natural fire regimes.

According to Kuuluvainen & Aakala's (2011) review, the gap (or patch) dynamic is prevalent in spruce-dominated stands and cohort dynamic in pine-dominated stands. Succession after stand-replacing disturbance occurs equally in both spruce and pine dominated stands. Although there are many exceptions, cohort structures can usually be found in pine-dominated forests and gap dynamics in spruce forests. Natural disturbances are bound to environmental conditions and in almost every case, even in the most intensive form, they leave many biological legacies, like survived old-growth trees or tree groups, untouched patches, logs and snags, organisms or seed banks, that form the next starting point and have a profound effect to the following succession (Lindenmayer & Franklin 2002, p. 56, Kuuluvainen & Aakala 2011).

Forest fires have traditionally been considered as the most effective and primary disturbance type in large parts of the boreal forest, especially in North America (Wallenius et al. 2005, Kneeshaw et al. 2011). This is evident in continental areas where dry summers and drought can lead to fire cycles as short as 50 years (Heinselman 1981, Hirsch 1991, Kneeshaw et al. 2011) but in many regions, like in Scandinavia and European Russia, where natural fire cycles are longer, other disturbances such as windthrow, insects, and fungi can play important roles (Kneeshaw et al 2011).

Forest fires differ in their size, severity, and return interval. In boreal Fennoscandia and western Russia, low- to medium-severity fires, such as surface fires are the most common disturbance type (Gromtsev 2002, Shorohova et al. 2009, Kneeshaw et al. 2011). Usually, more humid spruce (*Picea abies*) dominated areas have longer fire intervals than dry pine (*Pinus sylvestris*) dominated forests. Spruce stands are more prone to stand-replacing fires during drought periods, due to close-to-ground crowns and abundant foliage serving as fuel (Kneeshaw et al. 2011). According to Melekhovs (1947, cited in Gromtsev 2002) statistics, the share of surface fires account for 76-86% and crown fires for 16-24% of the total number of fires in western Russia. The occurrence of fires ranges from 1-2 times in a millennium to 1-2 times in a century depending on the landscape differences (Gromtsev 2002). The burned areas are typically relatively small due to fragmented landscape that offers many natural fire breaks (Wallenius et al. 2004).

In the absence of fire, other disturbance agents, like wind, insects, and fungi function as the drivers of forest dynamics. Usually these agents are connected to old-growth characteristics and small scale gap dynamics. Windthrow (uprooting) and windbrake (stem braking) are most common in areas with topography that has strong slopes or leads to wind-funneling and has species susceptible to damage (Kneeshaw et al. 2011). One susceptible species is the Norway spruce, with its long crown and shallow root system. Sometimes, ocean-originated autumn and winter storms can cause large-scale damage in coastal boreal Fennoscandia. The size of windthrows ranges usually from small gaps to few hectare openings but large-scale (e.g. cyclone Gudrun in Sweden) occurrence is possible. In North American studies, the stated return intervals are notably long, even thousands of years (Kneeshaw et al. 2011), but for Russian forests Schultze et al. (2005) and Gromtsev (2002) suggest return intervals of 150-300 years. Apart from

the mountain birch and the autumnal moth, there are no records of large-scale insect outbreaks in European boreal forests (Kneeshaw et al. 2011). Bark beetles or defoliating insects can cause significant local damage and rarely, together with some other disturbance factor (storms, drought) even large-scale tree mortality. Insects and fungi, for example root rot, are consequently more related to small-scale tree or tree group senescence and mortality. The occurrence of all disturbance agents are interrelated; fire or storms can make forests or individual tree susceptible to insects and fungi or vice versa.

1.3 Objectives and research questions

The general objective of this study was to investigate the historical variability of disturbances and their effect on the current forest structure and composition in unmanaged, naturally dynamic southern boreal forests. In the lack of suitable areas that are sufficiently large and free from human impact in the region of southern Finland, the research material was gathered from Russian Karelia. These areas are comparable to the environmental conditions in southern Finland. The target was to determine the disturbance frequency, intensity, and range in different spatial scales (plot, site/stand, regional). The more specific research questions can be formulated as: 1) How severe disturbances occur and how often? 2) What is the spatial scale of disturbances? (Do the disturbance chronologies differ by sample plot/site or are they similar?) and 3) Is there a connection between quality (severity, frequency, and scale) of disturbances and site characteristics (forest type or tree species composition)?

2 METHODS AND MATERIALS

2.1 Dendrochronology and dendroecological methods

The disturbance history of an area can be studied with dendrochronology and dendroecological methods. Dendrochronology is a discipline and a scientific method that uses tree-rings to record different environmental processes or events. It can be

applied to any environmental factor that directly or indirectly limits a process that affects the growth of ring structures. For example, it can be used to provide long-term records of past temperature, rainfall, fire, insect outbreaks, landslides, and storms or human-caused changes such as pollution or contamination (Speer 2010 p. 1). One of its strengths is the high (annual) accuracy and precision compared to many other environmental proxies such as pollen, ice cores, or lake sediments (Speer 2010 p. 2). The accuracy of dendrochronology is confirmed by crossdating the data. Crossdating refers to detecting the common year-to-year patterns of narrow and wide rings between trees and between sites which can be used to assign accurate dates to trees or tree-ring data that have no complete set of growth rings or the timing of death (year of last ring) is not known. Crossdating allows dendrochronologists to build up, even 15000 years, long chronologies (Guyette & Stambaugh 2003, Speer 2010 p. 8).

Dendroecology is a subfield of dendrochronology that uses tree-rings to study ecological events and processes such as succession, disturbance dynamics, synchronous masting, or movement of invasive species (Speer 2010 p. 189). Usually, the methods involve standard field and laboratory work that contain crossdating the samples and analysis of ring-width patterns, stand-age structure, tree establishment, or release dates and fire or other tree scars (Speer 2010 pp. 189-190). As opposite to dendrochronologists studying climate, in a dendroecological study, the climatic influence is usually a factor that needs to be filtered out, revealing the individual growth trends of a tree (Frelich 2002).

When investigating disturbance history, the most important part is to form a disturbance chronology for the study area. Building the chronology is based on detecting suppression and release events or seedling recruitment to gaps from the individual tree growth patterns. A release event is understood as an abrupt and sustained radial growth increase of a subcanopy tree that has been ‘released’ from the suppression of former canopy trees and that has now entered the canopy (Frelich 2002). Hence, the timing of release indicates the time of disturbance. This information is then gathered to build a disturbance chronology.

2.2 Site selection and study area

The expedition and field work in Russia was conducted in August 2015. The expedition was a joint venture with paleoecological research (Stivrins et al., manuscript, see EBOR p.37), and thus, the tree-ring sampling was linked together with collecting sediment cores from small forest hollows. Small hollows are small peat depressions inside closed-canopy forests that can be used to study local vegetation and fire history in paleoecological studies (Jacobson & Bradshaw 1981, Kuosmanen et al. 2014). The areas for the search of suitable sites were selected based on earlier paleoecological studies (Kuosmanen et al. 2014) and professional advice from project partners in the Karelian Research Center Biology Institute. The study areas are located in the Karelia Republic, Puutoisten district in northwestern Russia. The tree-ring data was gathered near the small hollows so that information from both sources could be used to reconstruct the disturbance history of the forest. We found four different small hollow sites suitable for taking sediment cores and to set tree-ring sampling plots. The plots had to be on mineral soil and major human influence, like clear-cutting, in the structure of the forest should not be visible. Some minor human influence like selective cuttings or evidence of pine tapping was accepted. Two of the small hollow sites were sediment sampled before in the previous study by Kuosmanen et al. (2014)(B and D in the Figure 1.) and two were new foundations (A and C in Fig. 1.). In the previously known sites, only the tree-ring samples and forest measurements were taken.

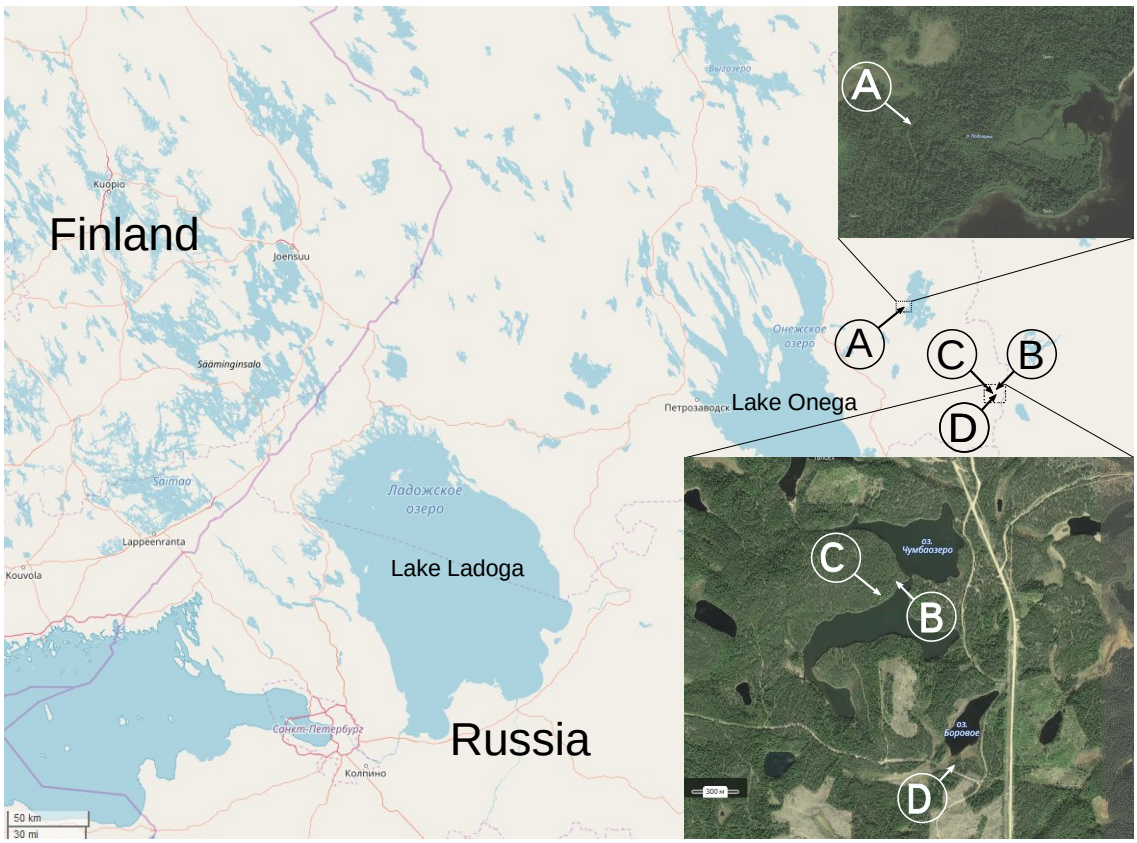

Figure 1: Map of the research area. A) Polttiainen, B) Larix hollow, C) Pine hollow and D) Olga hollow

The European Russian taiga zone extends from the Gulf of Finland and Russian-Finnish state border to the Ural mountains in the east. The western part of this area belongs to the Fennoscandian physico-geographic region in the Baltic crystalline shield, which is dominated by a denudation-tectonic hilly-ridge relief, with typical low-mountain areas and pine dominated stands (Gromtsev 2002). The eastern part belongs to Russian Plain with chiefly flat interfluves and a morainic-hilly relief, usually dominated by spruce stands. The north-south boundary between these two geographic regions goes near the administrative line between the Republic of Karelia and the Arkhangelsk province, which is relatively near our eastern sample plots. All our sample plots were in the middle taiga subzone in the Russian classification system (Gromtsev 2002) and in southern boreal zone according to Finnish classification by Ahti et al. (1968). (The Finnish subdivision is based on the thermal growing season, e.g. 160-175 days for southern boreal zone, Rantala 2007 p. 10). The mean annual precipitation in the Karelia region is 550-750 mm and mean annual temperature varies beween 0° C to 3° C from north to southern Karelia (Gromtsev et al. 2003, pp. 6-7).

In the Karelian region, the forest cover is formed by conifers such as *Pinus sylvestris*, *Picea abies*, *Picea abies ssp. obovata* (in the Russian nomenclature *Picea obovata*) and in the eastern side of the lake Ääninen also *Larix sibirica*. Deciduous species like *Betula pendula*, *Betula pubescens*, *Populus tremula*, *Alnus incana,* and *Alnus glutinosa* are usually present as a mix with confers but can dominate in recent gaps after disturbance (Gromtsev 2002, Shorohova et al. 2009). In the lake Vodlozero area, the forests are mostly spruce (*Picea abies ssp. obovata*) dominated stands but also pine (*Pinus sylvestris*) dominated stands occur. The ratio for pine and spruce stands is around 1:4 (Gromtsev et al. 2003 p. 49). The Vodlozero area was devastated by large-scale fires 350-400 years ago and the first generation of pine trees after the fire are still around in some intact forests. In moister and paludified stands, the pioneer deciduous species (*Populus, Betula*) were followed by spruce undergrowth and after the first, relatively coeval spruce generation, formation of uneven-aged stands with gap dynamics began (Gromtsev et al. 2003 p. 50).

2.3 Sampling

Our first small hollow site, named as Polttiais hollow (A in Fig. 2), is located in the southern part of the Vodlozero national park, in the western side of the Vodlozero lake (N62°16.559′, E036°45.092′ POL 1). Around the hollow, we established 5 tree-ring sampling plots in a 50 m grid so that the first plot was taken 15 m north from the center of the small hollow and the other four plots were 50 m from the center of the first plot to all major compass points (east, south, north, west). The southern plot was moved 20 m more south (70 m from the center of the first plot) because of a small bog. The forests in the area are mixed forests with uneven-aged structure and Norway spruce (*Picea abies ssp. obovata*) as a dominant species. The dominant trees belong to the narrow crowned subspecies of *Picea*, that is common in the continental and nothern parts of Siberia and the boreal zone. Other common tree species are silver birch (*Betula pendula*), downy birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*). Also some *Alnus*, *Sorbus* and *Populus* species were around but not in the canopy layer where the sampled trees were selected. Ground and field layer vegetation was typical for *Myrtillus* type mesic forests (MT, Hotanen et al. 2008). The spatial distribution, age and

species of sample trees from the five sample plots in Polttiais hollow are shown in Figure 3.

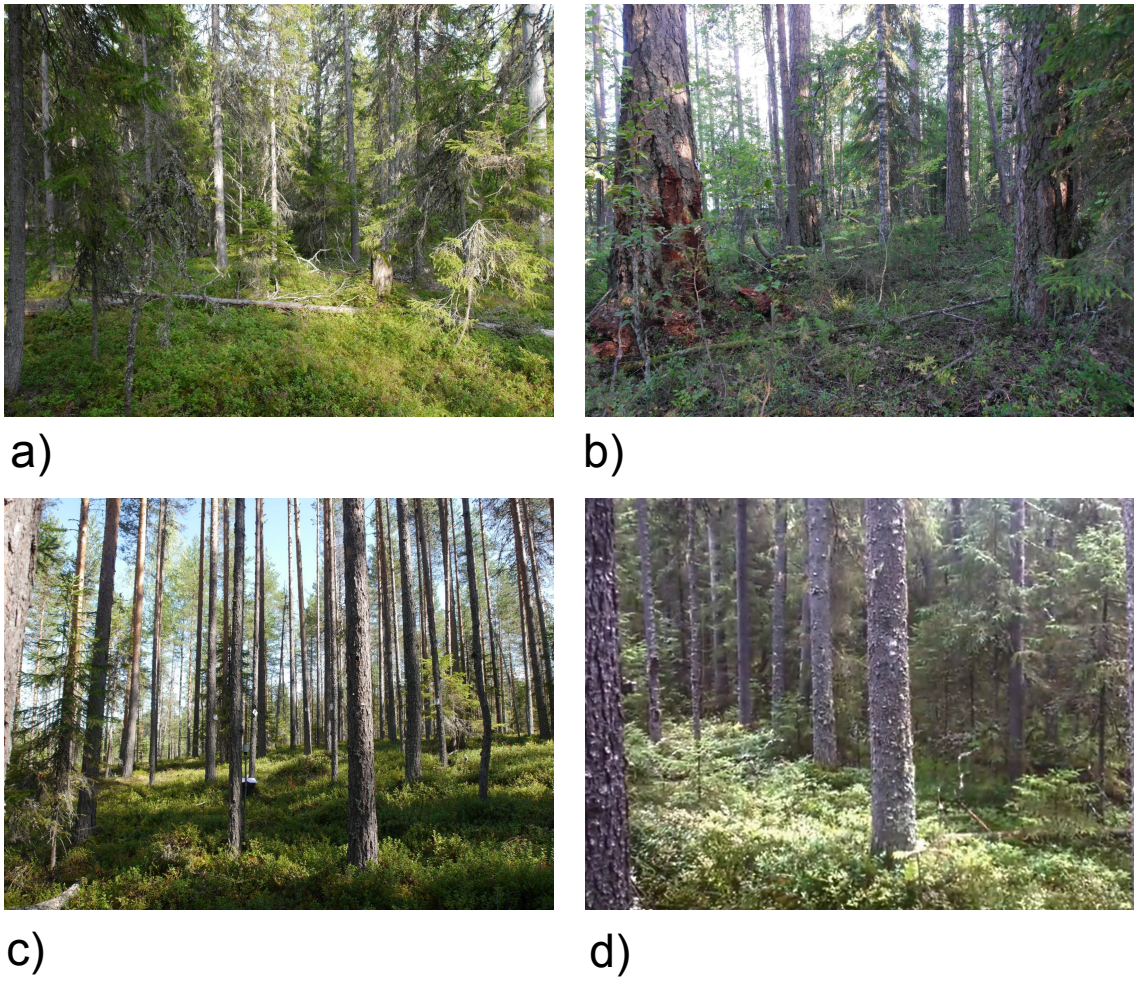

Figure 2: General view from the study sites a) Polttiais hollow b) Larix hollow, c) Pine hollow and d) Olga hollow

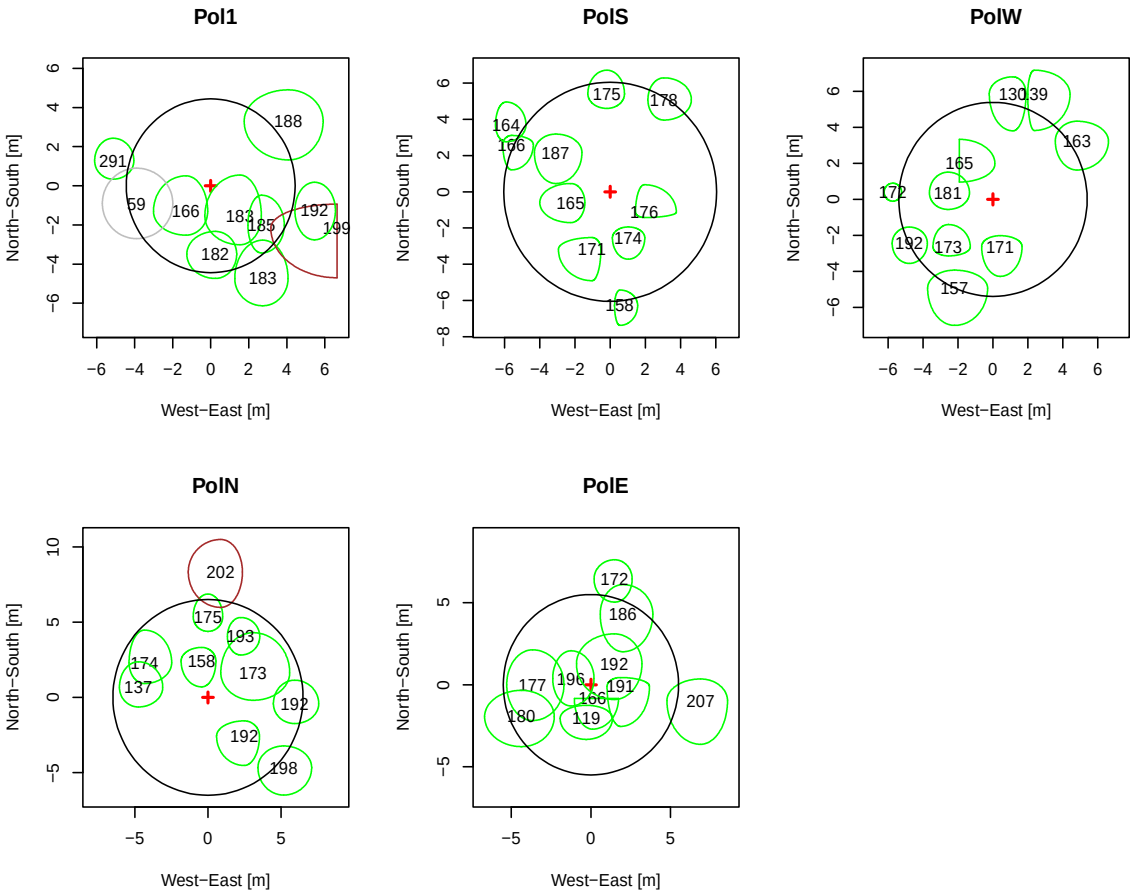

Figure 3: Tree crown maps of Polttiais hollow (Pol1, PolS, PolW, PolN, PolE). The colours of the crown shapes illustrate tree species: green = spruce, brown = pine, gray = birch and blue = larch. The number in the center of crown is tree age. Black circle represents the border of a plot.

Our second sampling site was Larix hollow (B) (N61°50.753′, E037°45.394′ LAR 1), approximately 80 km south-east from the Vodlozero lake. Larix hollow is a small peat depression between a lake and a slope. It is surrounded by mixed forest, with spruce, birch, pine, and Siberian larch (*Larix sibirica*) as the main species. The ground and field layer vegetation indicated herb-rich heat site (*Oxalis-Myrtillus* type) and mesic forests. We managed to fit only three tree-ring sampling plots to the site due to geographical and human influence restrictions on the surrounding forests. The sampling plots LAR 1-3 were established in a line to south-west (210°) from the hollow with distances 15, 50 and 100 m respectively. The spatial distribution, age and species of sample trees from Larix hollow are shown in Figure 4.

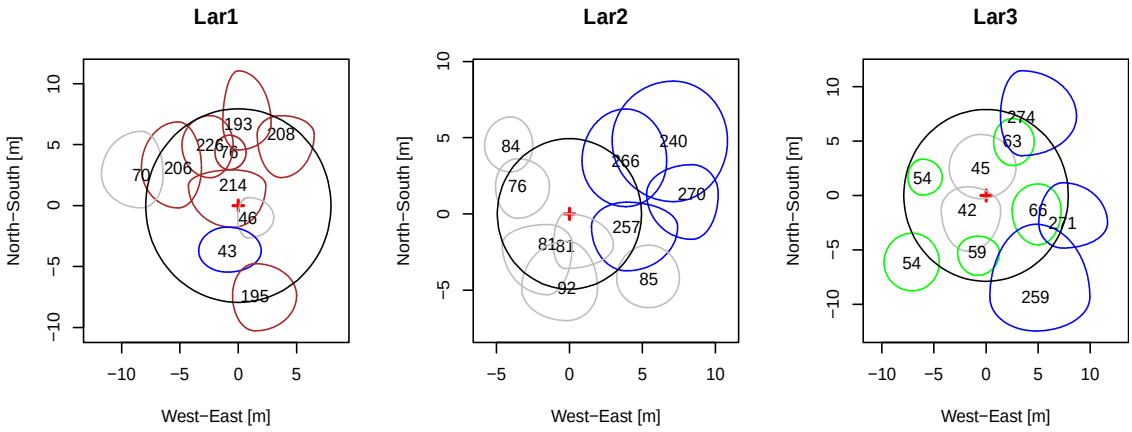

Figure 4: Tree crown maps of Larix hollow (LAR1, LAR2, LAR3). The colours of the crown shapes illustrate tree species: green = spruce, brown = pine, gray = birch and blue = larch. The number in the center of crown is tree age. Black circle represents the border of a plot.

Third site, named as Pine hollow (C) (N61°50.710′, E037°45.303′ PIN 1), is a small hollow between forested, pine dominated slopes and a lake. The pine forests were seemingly even-aged and some marks of selective cuttings were visible. Few spruce and downy birch saplings were in the field layer. Ground and field layer vegetation was typical for a sub-xeric *Vaccinium* type forests (VT, Hotanen et al. 2008). Partially abundant *Calluna vulgaris* occurrence could be an implication from past forest fire. Only three sampling plots (PIN 1-3) could be set to the site because of forestry roads and recently made clear-cuttings near the hollow. The plots were arranged to an east-west oriented line so that the first plot was 15 m east from the center of the hollow, second 50 m east from that and the third 50 m west from the hollow. Three additional corings were made from two large pines and a larch outside the sample plots to get backing information from older generation trees.

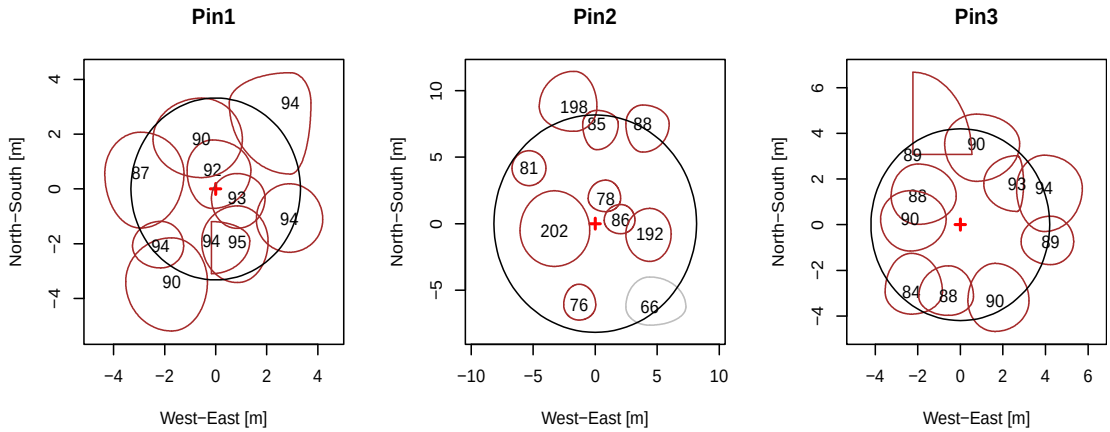

Figure 5: Tree crown maps of Pine hollow (Pin1, Pin2, Pin3). The colours of the crown shapes illustrate tree species: green = spruce, brown = pine, gray = birch and blue = larch. The number in the center of crown is tree age. Black circle represents the border of a plot.

Our last sampling site was Olga hollow (D) (N61°50.143′, E037°45.856′ OLGA 1) in the northern part of Puutinen district. It is a narrow peat depression between two forested slopes connected to a mire. On the surrounding slopes of mineral soil, pine and spruce dominate, mixed with birch and tall larch trees. In some plots, there was two or three cohorts, with old birch and larch trees at low incidence in the upper canopy and spruce and deciduous poles or saplings in the subcanopy layers. The ground and field layer vegetation indicated *Myrtillus* type mesic forests (MT, Hotanen et al. 2008). We managed to fit only three sample plots to the site because of a surrounding mire and human influence restrictions. The sampling plots OLG 1-3 were established in a line to north-west (300°) from the hollow with distances 15, 50 and 100 m respectively.

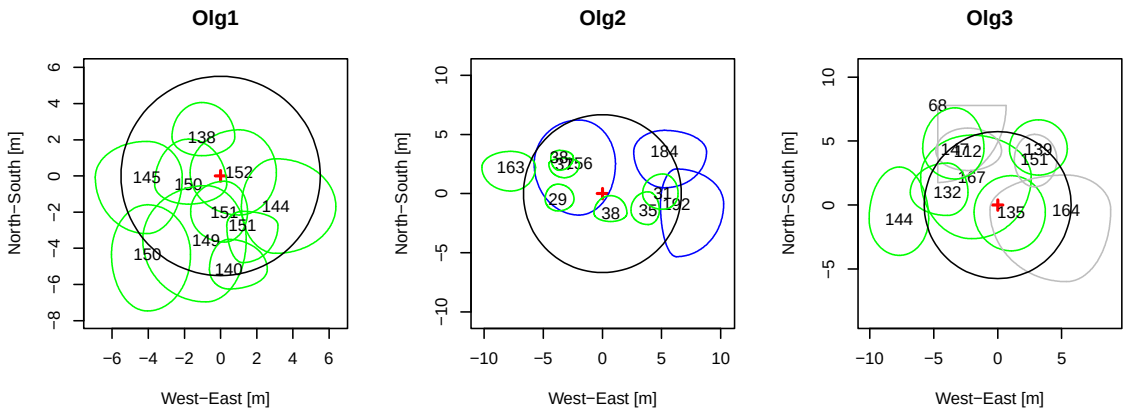

Figure 6: Tree crown maps of Olga hollow (Olg1, Olg2, Olg3). The colours of the crown shapes illustrate tree species: green = spruce, brown = pine, gray = birch and blue = larch. The number in the center of crown is tree age. Black circle represents the border of a plot.

From every sample plot, we gathered information about vegetation, human influence, and recent disturbances (stumps, windthrows, dead wood, insects etc.). In a plot, we chose 10 sample trees from the canopy layer based on the crown distance from the center of the plot (ten nearest were chosen). A tree was considered part of the canopy if the crown was receiving direct sunlight from above. Border of the plot was determined by the distance from the center of the plot to the 11th canopy tree crown. Consequently, all the sample plots have different diameter and area, the areas ranging from 35 to 210 m^2. Trees under 10 cm diameter or dead trees were not sampled. From the sample trees, we measured diameter at breast height (DBH), height, crown drip line distances in four major compass points from the stem (to calculate canopy projection area), and basal area of the stand separated by tree species. For these measurements, we used a tallmeter, a laser distance measurer and a relascope. Each sample tree was cored at 50 cm height using a tree increment corer. In cases where the tree was tilted or the trunk was somehow abnormal, the height was adjusted to get a proper sample. As part of the joint research, fire scars were sampled from trees near the sites to get additional evidence from possible forest fires (Stivrins et al., manuscript). An example of the field form used in the expedition can be found in the Appendix 1. The main attributes of all the study sites are given in Table 1.

Table 1: Main attributes of the four study sites.

Site	Forest type	Dominant tree species	Location	No. of plots/ sample trees
Polttiainen	MT	Norway spruce	N62°16.559′, E036°45.092′	5 / 50
Larix	OMT/MT	Norway spruce, Silver birch, Scots pine, Siberian larch	N61°50.753′, E037°45.394′	3 / 30
Pine	VT	Scots pine	N61°50.710′, E037°45.303′	3 / 30
Olga	MT	Norway spruce, Silver birch, Siberian larch	N61°50.143′, E037°45.856′	3 / 30

2.4 Tree-ring data and analysis

The increment cores from the sampled trees were stored inside paper straws and transported to Finland for analysis. Every sample was carefully removed from the paper straw and glued onto core mounts. Unfortunately, some of the samples were broken into small pieces during the transportation. Fragmentation does not prevent from using the sample but it increases the risk of missing or misplaced rings. After drying, the surface of the samples were sanded to make the annual rings more visible. All the samples were then scanned and tree-ring widths were measured with WinDENDRO software (Regent Instruments Inc., Quebec, Canada). The deciduous birch samples and some unclear cases of conifers were also marked and checked manually with a stereo-zoom microscope to make sure ring counting was accurate. Age corrections were calculated to all the samples that did not have the actual pith in the sample by estimating the width and number of missing rings with a pith locator (Applequist 1958). The ring-width data was then further analyzed and crossdated with the help of COFECHA program that is designed to assess the measurement accuracy of tree-ring series and quality of crossdating (Grissino-Mayer 2001).

2.4.1 Detecting growth releases from increment cores

The growth curve from all the 140 sample trees was analyzed to detect and date release and recruitment events from individual trees. In this study, two common methods that are well established in dendroecological literature were used simultaneously: The radial

growth averaging criteria (percent-increase method) from Nowacki & Adams (1997) and the absolute increase method from Frawer & White (2005b). The objective criteria of these methods were used together with subjective evaluation. If the growth curve was typical for a tree that has grown in relatively open space (close to negative exponential distribution or descending trend), and there was no evidence of release events, the tree was considered born as a seedling recruitment to a gap (see examples in Fig. 7 and 8). In the chronology, this is interpreted as an indicator that the disturbance has happened just before the tree was born. Here should be noted that because the trees were cored on 50 cm height, the actual tree age is greater than presented in this study. All the tree ages expressed in this study are recruitment ages at the height the trees were cored. As we did not use any correction factors to estimate the actual tree ages, also the year of disturbance event is some years earlier than presented in the chronology (gap origin trees).

In the standard percent-increase method, the principle is to make running comparisons of ring-width averages in a certain, usually 10-20 years, time window to point out years when the set threshold for a growth release is crossed (Equation 1).

$$\text{percent increase} = \text{Mean}_{t2} - \text{Mean}_{t1} / \text{Mean}_{t1} * 100 \quad (1)$$

In the equation, Mean_{t1} is the mean radial growth during the time window prior to the event, and Mean_{t2} is the mean radial growth following the event. The 10-20 year long time window is needed to filter out the growth response to short-term changes in temperature and precipitation (Nowacki & Adams 1997). In many studies, thresholds of 50% for minor release and 100% for major release have been used (Frelich 2002) but in this study only 100% criterion was considered functional because it was found better comparable with the absolute increase method and it better indicates access to the canopy layer. For both methods, a 10-year time window was used. In detecting the release, the maximum percentage growth change in each 'release' pulse was used to date the disturbance (Svoboda 2011).

In the absolute increase method, the post-event growth rate is subtracted from the pre-event date (Equation 2). If the difference exceeds a predetermined species-specific threshold, the event is considered a release. Using a constant threshold makes the

release criterion more stringent at low rates of prior growth and more lenient in relatively high rates. This helps to correct the known shortcomings of the standard percent-increase method (Fraver & White 2005b).

$$\text{absolute increase} = \text{Mean}_{t2} - \text{Mean}_{t1} \quad (2)$$

Since we didn't have any prior knowledge or data sets from trees in the study area, we calculated the standard deviations (SD), 1.25 x SD, and 90 % quantile of the absolute increases to select the species-specific increase thresholds (Table 2). Use of 1.25 x SD or 90 % quantile thresholds is recommended for unfamiliar data sets by Frawer & White (2005). After some testing and evaluation, the 1.25 x SD turned out to be better suited, giving less false-positive and false-negative releases for this data.

Table 2: Attributes for release detection in the absolute increase method.

Species	Mean ring width mm	1.25 x SD (mm)	90% quantile	No. of cores
Picea abies	0.65	0.32	0.24	74
Pinus sylvestris	0.72	0.37	0.33	37
Betula pendula	1.00	0.42	0.29	17
Larix sibirica	0.83	0.33	0.19	12

After testing and calibration of these methods and thresholds, our final criterion for a release was formulated so that at least one of the methods (% or absolute) indicated a release *and,* in the growth trend, there was clear and sustained, at least 20 years, increase in the growth level. The cases where the threshold for release was exceeded because of early years growth spurt (and the growth trend was close to negative exponential curve) or the release was indicated right after a short period of minimal growth (probably due to some anomaly in climate conditions), were interpreted as false-detections. In borderline cases, for example when the growth trend was parabolic or gradually rising, a conservative interpretation (not a release) was used. Irregular growth patterns, such as patterns with many peaks that met the release criterion, were determined case by case. All the analysis for growth trends and release detection was

made using R-program (version 3.4.2), a free software environment for statistical computing and graphics.

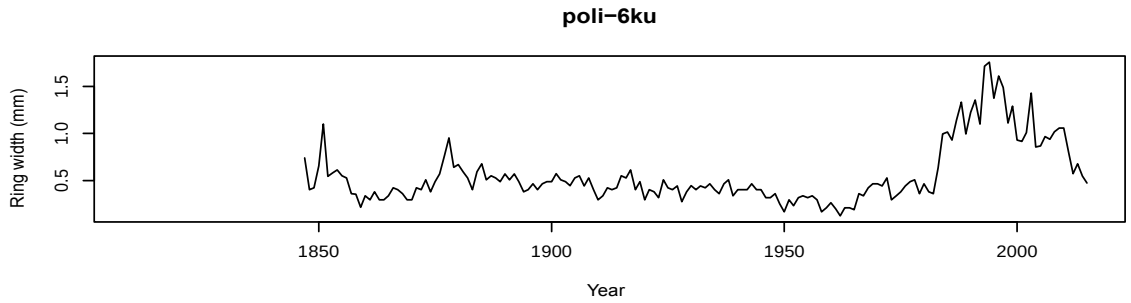

Figure 7: Example of a release in growth trend. A 177 year old spruce tree (poli-6ku) from Polttiais hollow. In the x-axis years and y-axis ring width (mm).

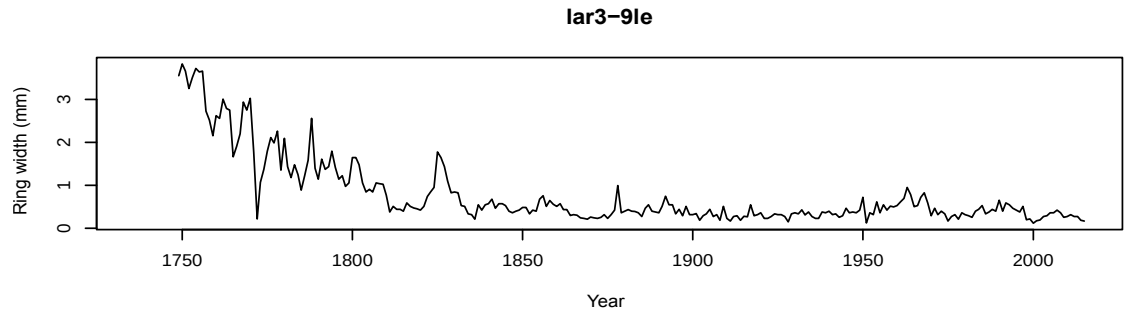

Figure 8: Example of a gap born tree growth curve. A 271 year old larch tree (lar3-9le) from Larix hollow. In the x-axis years and y-axis ring width (mm).

2.4.2 Preparing disturbance chronologies

The releases and recruitment events were integrated to form a disturbance chronology for each plot. The events were tallied by decade to account for the possible delay between a disturbance and a tree's response (Lorimer & Frelich 1989). To be able to examine the occurrence of disturbances on different spatial scales, the results are pooled by plot, site (stand), and all sites. When interpreting the tree age class distributions and disturbance chronology, it should be taken into account that it may take a long time for a suppressed tree to reach the 10 cm DBH limit (Aakala et al. 2010) and the establishment of trees smaller than that are not detected.

The similarity of the decadal disturbance patterns between sites was measured with the Bray-Curtis dissimilarity metric (Svoboda et al. 2013). The dissimilarity values are bound between 0 and 1, where 0 means that the two sites have the exact same temporal pattern of disturbance severity and 1 means that the sites do not have any disturbances at the same decades. The Bray-Curtis dissimilarity was calculated as follows,

$$BC_{ij} = \frac{\sum_{d} |S_{id} - S_{jd}|}{\sum_{d} S_{id} + \sum_{d} S_{jd}} \quad (3),$$

where *i* and *j* are the compared sites, *d* is the decade in question and S is severity(%) of the *d*th decade.

To get a better understanding of the spatial extent of the disturbances, we estimated the disturbance rate (%) per decade for each site. Disturbance rate is defined here as the proportion of the disturbed canopy area per decade. In the scientific literature, two common ways of calculating the disturbance rate is used, the other using total canopy area (canopy cover) as baseline, and the other land area (Frelich 2002, Fraver & White 2005, Svoboda et al. 2013). To allow better comparison with other research and between sites in this study, we decided to express the disturbance rate in both ways, as a percentage value of land area and total canopy area (Fig. 12). The canopy area based values are presented only for comparison purposes and the land area based values are considered the actual results that are reported and discussed in the relevant chapters. Since knowledge on the canopy cover (%) affects the interpretation of the disturbance rate, also these figures are presented along with the disturbance rate results.

We estimated the canopy projection area of a sample tree by first calculating the four areas of a quarter ellipses based on the four measured crown directions and then summing the quarter ellipses together (Fraver & White 2005, Lorimer & Frelich 1989). The overlapping canopy projection areas and crowns growing outside the plot border were counted out from the disturbed area. The summed canopy projection areas were then used to calculate the disturbed area per decade for each plot. The canopy disturbance rate estimate is based on an assumption that the individual canopy projection area of a tree corresponds to the area of the original disturbance (Frelich

2002). The calculated disturbance rates will inevitably underestimate recent decades because many gap-recruited trees have not achieved the diameter for coring and the use of 10-year post-disturbance window for release detection cuts the data to year 2005 (Frelich 2002). All the analyses were made with R-program using maptools, PBSmapping, sd, spdep, and rgeos packages.

To better quantify the rate of the disturbances (over decades) per plot we calculated a disturbance index (DI) for all the plots, as applied by Svoboda et al. (2013). The disturbance index represents how diffuse or clustered the disturbances are and allows us to give a more descriptive single value to the characteristic disturbances in an area, than the average of the disturbance rates (%) over decades (Fraver & White 2005). The disturbance index is based on the Shannon index as follows,

$$DI = \sum_{i=1}^{N} p_i \log p_i \qquad (4),$$

where p_i is the proportion of canopy area disturbed belonging to the *i*th decade and N is the number of decades. The maximum theoretical values of the index reach from 0 to ca. -3, where 0 indicates 100% canopy area disturbed in a given decade (all the observed disturbances have been clustered to one decade) and -3 indicates similar canopy area disturbed in all decades.

3 RESULTS

3.1 Current forest composition and structure

From the studied forest sites, two (Polttiainen and Olga) were spruce-dominated stands and one (Pine) pine-dominated stand. One stand (Larix) represented mixed-forests with quite even mix of pine, larch, spruce and birch trees. None of the sites were pure one-species stands, always having some mix in the canopy layer trees. The average basal area and number of sample trees by species are reported in Table 3. The overall (all species) basal area varied between 22.1-27.3 m^2/ha in the four sites. The diameter class distribution from all the sample trees was descending, reversed-J character, having quite a long tail with the largest trees. (Fig. 9).

Table 3: Average basal area by species and sample trees by species.

	Basal area by species m^2/ha				Tree species (No. of trees/site)			
Site	Picea	Pinus	Larix	deciduous	Picea	Pinus	Larix	Betula
Polttiainen	18.4	3.5	0	1.9	46	2	0	2
Larix	4.9	6.1	6.1	5.8	5	7	8	10
Pine	0.4	25.8	0.3	0.8	0	29	0	1
Olga	15.8	0.7	1.4	4.2	23	0	3	4

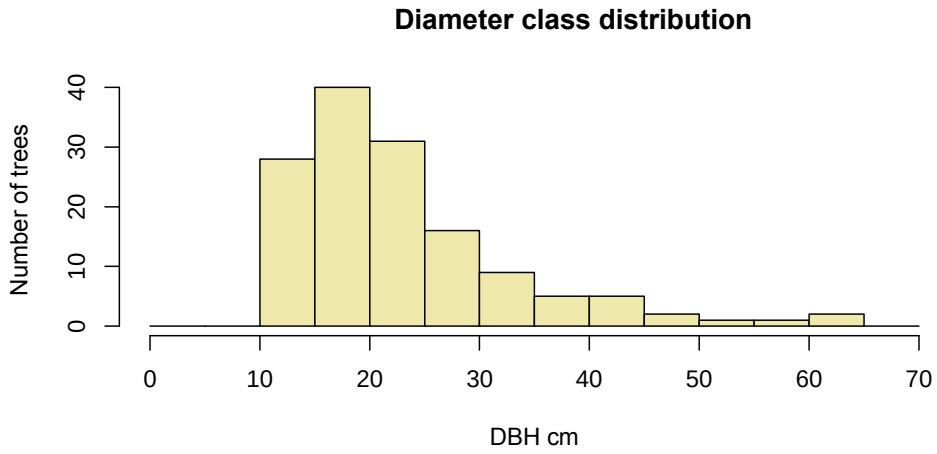

Figure 9: Diameter class distribution of all 140 sample trees. In the x-axis diameter at breast height (DBH) in 5 cm classes and in the y-axis number of trees. Trees under 10 cm diameter were not sampled.

The age structure of the forests was uneven-aged in almost all of our study sites (Figure 10). As a clear exception was the Pine hollow with relatively even-aged trees, where ages were mostly between 80-100 years. Albeit, there were some trees left from the prior ~200 years old generation. The oldest tree from all the cored trees was from Pine hollow (one of the extra trees) with the age of over 408 years. In the age class distribution of all the sample trees, the range was from 29 to 291 years and the majority of trees were around 150-200 years old. Trees from Pine hollow form the distinctive peak in the 90-100 year age class.

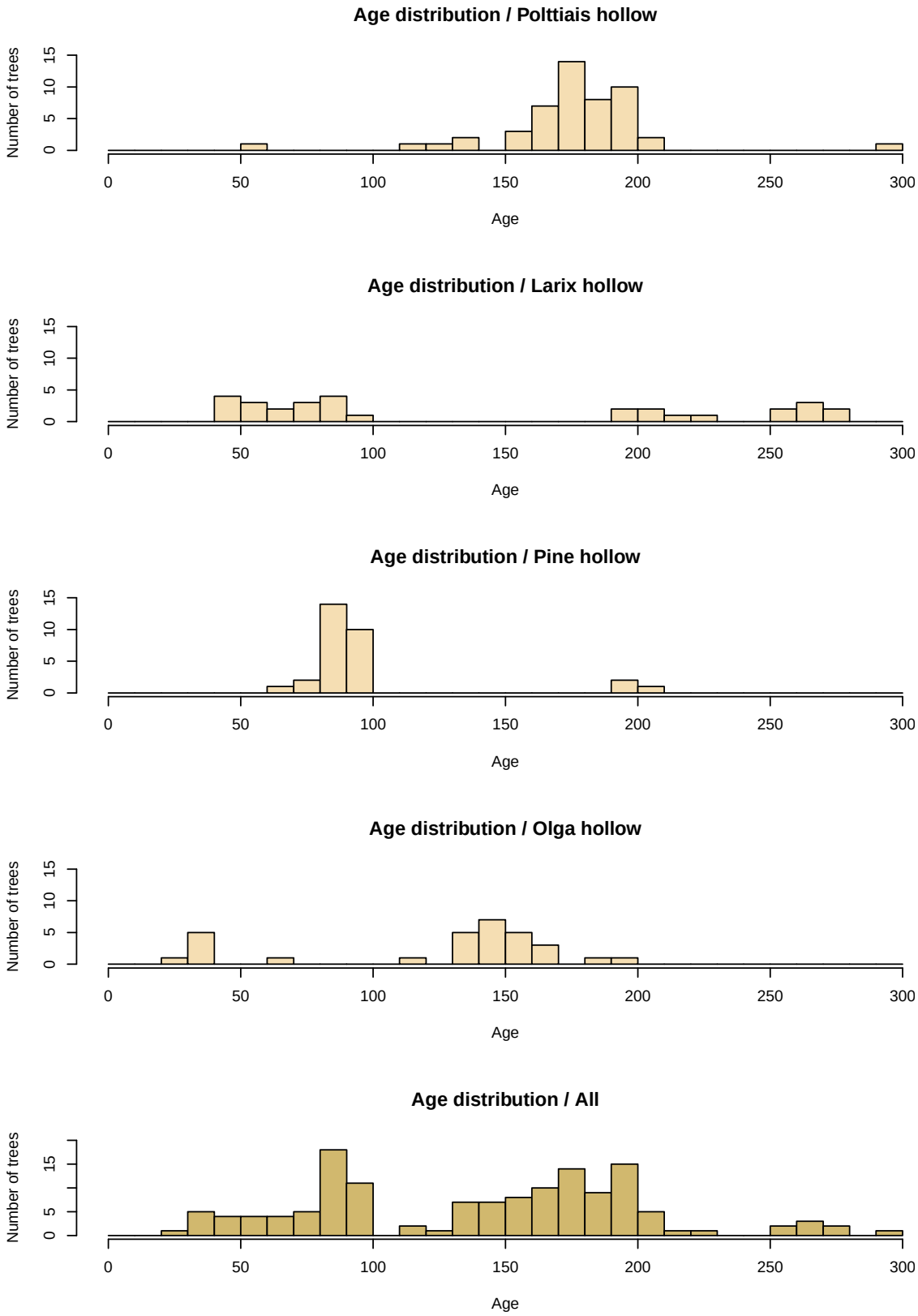

Figure 10: Age class distribution of all four sites (Polttiainen, Larix, Pine, Olga) separately and all sites pooled (140 sample trees). In the x-axis age by ten year classes and in y-axis number of trees.

The age class distribution from Polttiais hollow is quite unimodal, concentrating in age classes between 160-200 years. Almost all the trees were spruce trees with very slow growth and relatively small diameter. In Larix hollow, there seemed to be two or tree cohorts of trees, (interpreted with relatively wide time windows), the youngest cohort being around 50-100 years old, the middle around 200 years and the oldest over 250 years. The oldest trees were all huge larch trees, the middle cohort was purely formed by pines and the youngest cohort was a mix with birch and spruce trees. Interestingly, the age classes from 100-200 were almost totally missing, similar to Pine hollow. In Olga hollow, most of the trees were in 130-170 year age classes, only a few trees were approaching 200. All the younger trees were from one plot that happened to be right in a newly formed canopy gap with lot of young saplings of spruce and deciduous species with different ages. The older cohort was a mix with spruce, larch and birch trees. It is worth noticing that there were several over 150 year old birch trees forming the canopy.

3.2 Disturbance chronologies

From the 140 sample trees, 69% (97) of the trees indicated gap origin and 29% (41) indicated a release. (Two of the samples had to be excluded from release analysis due to decayed parts). In the pooled disturbance chronology, majority of the release events have occurred in the four recent decades whereas gap born trees have emerged in most of the decades. In Pine and Olga hollow, the ratio for releases and gap recruitment is close to the overall ratio but in Larix hollow, the figures for release and gap recruitment are 10% and 87% and in Polttiainen 42% and 58%, respectively. When looking at the site (or plot) specific chronologies, there is significant variation in timing of the disturbances between sites and plots. This is also confirmed by the Bray-Curtis metric, with all the site-specific dissimilarity values ranging from 0.75 to 0.94 (appendix 3). The disturbance chronologies by site and all sites pooled together are shown in Figure 11. For practical reasons, the individual plot chronologies are presented in the Appendix 2.

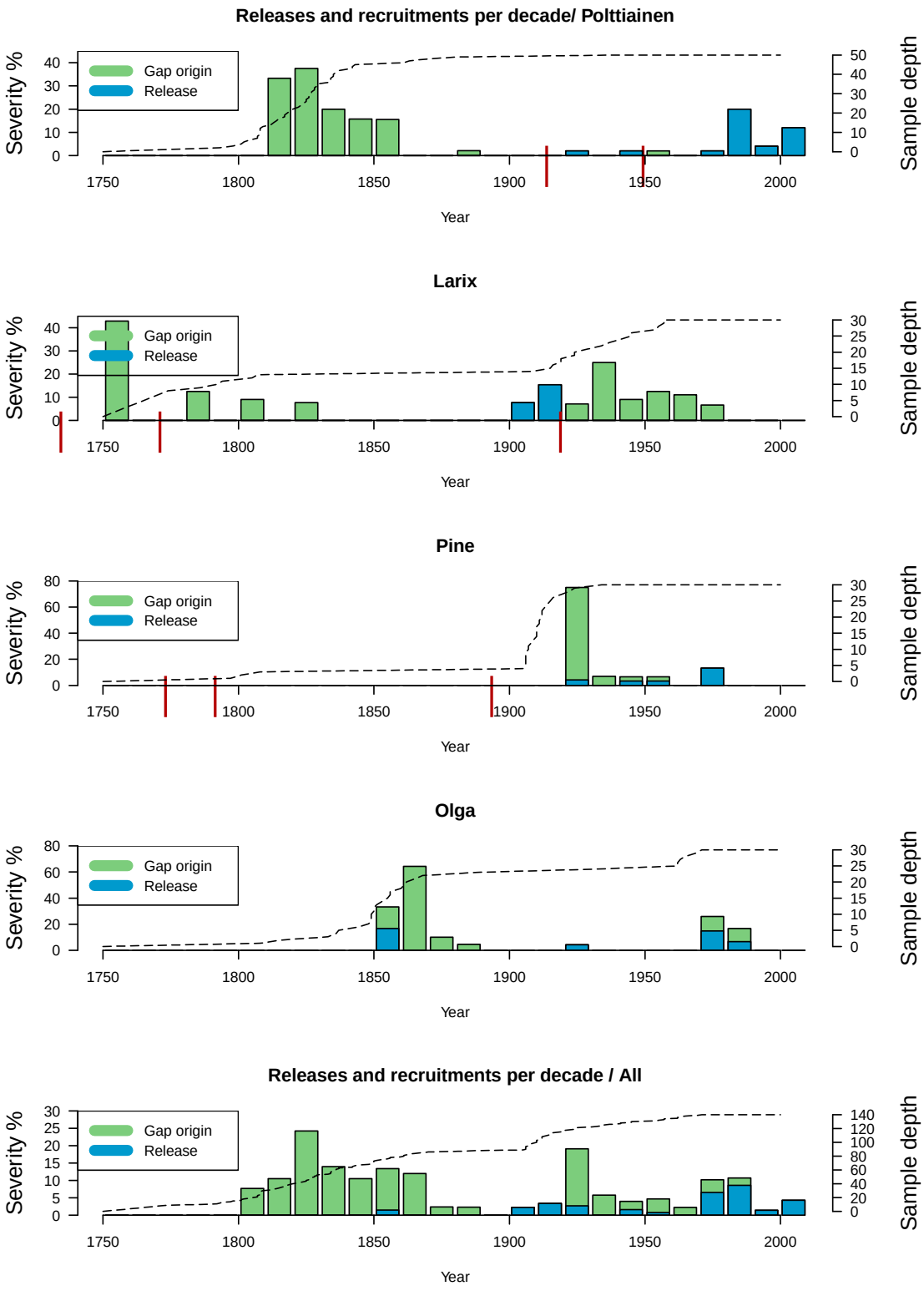

Figure 11: Disturbance chronologies on a decadal scale. First, all four sites separately and then pooled together. In the x-axis years and in the (left) y-axis % of trees indicating a release or a gap recruitment. The sample size contributing to the chronology is shown as a dashed line with corresponding values on the right y-axis. The chronologies are truncated after sample size drops below 5 in individual sites and 10 in the pooled chronology. Red vertical lines represent the dated fire scar years from the site in question.

In Polttiais hollow, the disturbances cluster in two time spans, the first between years 1820-1860 and the second between 1980-2005. The first cluster, with several gap recruitments, can be seen with different magnitudes in all of the plots. The later cluster with mostly releases is visible in three of the plots (PolN, PolE, and PolS). Since almost all of the sample trees are aged between 150-200 years, which suggests that they are born after a stand scale (or larger) disturbance or sequential disturbances in the beginning of 19th century (the first cluster) and some smaller scale disturbance in recent decades (the second cluster), have helped suppressed trees get to the canopy layer.

In Larix hollow, the timing of disturbances is scattered over many decades and the chronology should be interpreted together with the age and species information. The first peak between 1740-1760 is the time when all the sampled larch trees have been recruited. All the single recruitments around the turning of the 1800s and trees showing releases are pines that belong to same age group and are from the same plot (Lar1). In the growth trends of the released pines, there are several releases, suggesting that releases could be more related to self-thinning or pine tapping than getting access to the canopy. All the large pines from plot one (Lar1) had marks of pine tapping. The minor peak in the chronology in the 1940s, and the adjacent decades, show recruitment of spruce and birch trees in all of the plots. This is probably caused by small-scale disturbances and regeneration due to sporadic die back of the old, dominant larch and pine trees. As evidence, in all of the plots, there were single large trunks of downed or standing woody debris. One of the fresh, larch windfalls was sampled and it turned out to have died just a year before our expedition (2014) and belonged to the same age group as the dominant larch trees.

The disturbance chronology in Pine hollow shows one distinctive peak in the 1920s, at the time when almost all of the sampled trees were recruited. Most of the releases are also timed around that decade, with exceptions in plot 3 (Pin3) where four of the trees show a release during the 1970s. These exceptions could have been caused by selective cuttings, since those trees were near two large stumps in the plot. The examined extra two trees near the first plot that belonged to the older generation of tees (240-255 years old), showed also releases just before the peak in the 1920s.

In Olga hollow, the disturbance chronology shows two peaks in disturbances, the first between years 1850-1870 and the second in 1970-1990. The first peak is evident in all of the plots and the latter at least in two of the plots (Olg2, Olg3), the first plot (Olg1) indicates only one release to that time and considering the trees location near two standing dead snags, it could be just a coincidence and not related to the other plots. All the trees in the first peak are gap recruited and in the second peak, there are both gap recruited and released trees. It seems that all of the sample trees originate from a stand scale disturbance that happened before the 1850s but the later disturbance has been more local, affecting mainly two of the plots. In Olg2, the 1970-1990 disturbance has made a distinctive canopy gap with abundant regeneration, whereas in Olg3, most of the original trees have survived and benefited from minor gap openings or boundary effects.

3.3 Disturbance rate

To get a better understanding of the spatial extend of the disturbances, we calculated the decadal disturbance rate (%) for every plot and site (Figure 12). Since the study forests have considerable differences in their structure and dominant species, the average canopy cover percentages (%) for each site are given here as a reference. The Polttiais hollow with narrow crowned spruce trees had the lowest canopy cover, only 39%, in Larix and Pine hollow the average canopy cover was 63%, and in Olga hollow 70%. (Note that these are also the maximum values that the site specific area based disturbance rates can reach).

In general, the overall decadal rates of disturbance were quite low, varying between 0-11% in the all sites pooled data. In Polttiais hollow, the range was 0-8%, with many undisturbed decades and ‘peaks’ or clusters similar to the chronology in Fig. 11. The Larix hollow had range of 0-12%, Pine hollow 0-43% and Olga hollow 0-24% in the decadal disturbance rate. The tree population based (severity) and area based (disturbance rate) chronologies resemble each other substantially in all spatial scales, so the spatial dimension adds little new evidence to our examination. The few notable differences in the weighing of some decades in Larix hollow indicate decades with many wide crowned birch or larch trees. The calculated plot-specific disturbance

indexes for Polttiainen, Larix, Pine and Olga hollow ranged from [-1.8, -1.2], [-1.7, -1.4], [-1.7, 0], and [-1.3, -1.0], respectively (Appendix 3).

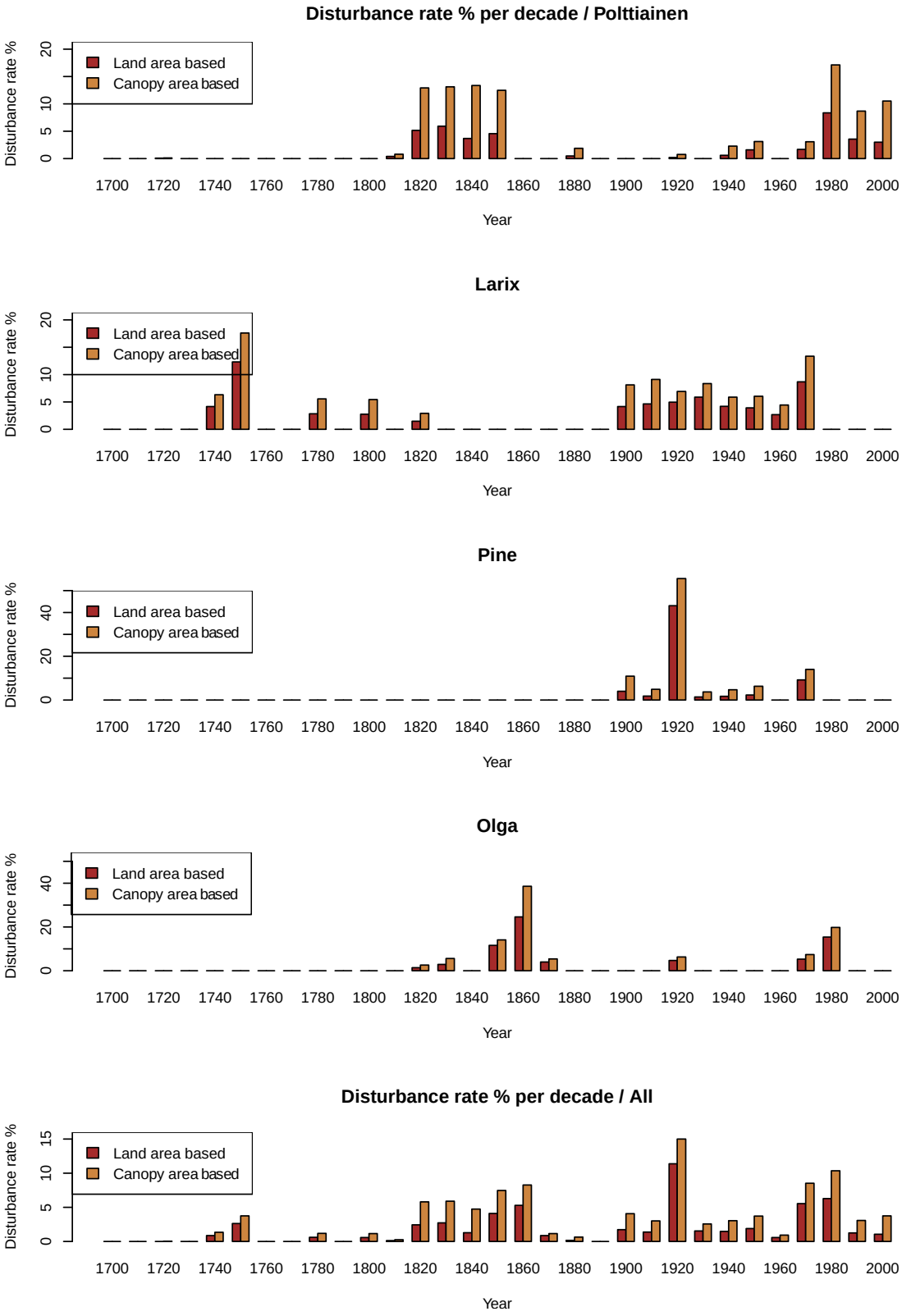

Figure 12: Disturbance rates for study sites separately and all pooled together. In the x-axis decades and y-axis disturbance rate %. Red bars present rates per total forest area and brown bars per canopy area.

4 DISCUSSION

We reconstructed the disturbance history of four different sites in southern boreal forests of Russian Karelia. The disturbance chronologies showed significant variation in spatial and temporal scales between sites and sample plots, reflecting the differences in forest type and species composition. During the 22-26 decades of observation, all the sites had low (0-20%) to moderate (20-40%) or low to high severity (>40%) disturbances (classification by Frelich & Lorimer 1991). It is probable that at least three, or possibly all, of the study sites have gone through a stand-scale disturbance during the last three centuries. In the overall chronology, the decadal severity (percentage of trees showing release or gap recruitment) of disturbances ranged from 0-25%. These results are congruent with the suggested surface fire disturbance regime (Kneeshaw et al. 2011) and the prevalence of low to medium severity fires in Russian Karelia (Gromtsev 2002, Shorohova et al. 2009).

When comparing the spatiotemporal pattern of disturbances, it seems that there was no synchronization between sites, but the plots in a site were synchronized to some extent. The dissimilarity of sites is confirmed by the Bray-Curtis metric that gives values close to 1 for all pairwise site comparisons. Some similarity is found between the two spruce-dominated stands (Polttianen & Olga), since the pattern of disturbances have the same form but timing of events is slightly different. When the chronologies are pooled together, representing regional or landscape scale, the disturbances are scattered to all of the decades, hence the timing of disturbances differs between sites. This suggest that during the last centuries, there was no regional scale disturbances.

In the site-specific chronologies, the temporal disturbance pattern is always more or less clustered to 1-4 decades, leaving many decades (8-15) with little or no evidence of disturbance. Large temporal fluctuation and clustering of disturbances have been reported in several disturbance history studies (see e.g. Fraver & White 2005, Fraver et al. 2008, Svoboda et al. 2013, Trotsiuk et al. 2014). The observed disturbance clusters could be the result of related consecutive disturbances such as windthrow plus insects or a prolonged regeneration span following one high severity disturbance (Fraver et al.

2008, Svoboda et al. 2013). For example, several decades long recruitment span for *P. abies* has been suggested in many previous studies in boreal, temperate and mountainous forests (Holeksa et al. 2007, Fraver et al. 2008, Svoboda et al. 2012).

The two different ways (population and area based) of building disturbance chronologies have both been frequently used in dendrochronological studies (Lorimer & Frelich 1989). In the population based (severity/intensity) chronology, the weight of recent decades can get exaggerated because of the dense, young trees/saplings having the same weight as older trees. This bias can be avoided using tree crown projection area based disturbance rate (Frelich 2002, Trotsiuk et al. 2014). In this study, the severity and disturbance rate chronologies had no significant differences in pattern and importance of different decades but the % values are somewhat consistently higher in the severity chronology. The similarity in pattern and importance is probably due to small amount of gaps and young trees in our plots and also the fact that most of the sites had trees with similar crown area (only a few deciduous, wide-crowned trees).

The calculated disturbance rates (disturbed canopy projection area % of land area) may seem low, considering that at least in three of the sites majority or the trees originate from the same disturbance pulse. For example, in Polttiais hollow, during the four decades when all the sample trees were recruited, the disturbance rate never goes over 10%. The explanation to this is purely methodological. The land area based calculation does not take into account the interstitial space between trees, that can be quite substantial in some boreal forests. In the Polttiais hollow case, we have only information of 39% (canopy area) of the land area, leaving 61% out of scrutiny. This can also hinder the detection of releases from tree-ring data (Fraver et al. 2008). Some of the interpretation problems related to low canopy cover, could be avoided using the canopy area based calculation (see e.g Svoboda et al. 2013, Trotsiuk et al. 2014), that gives better opportunity to compare between different forests/stands but at the same time loses information on the interstitial spaces that could potentially be part of the forested habitat in some other time perspective (that may not be recorded in the lifetime of the sampled trees). Furthermore, the land area based values are more comparable to the rotation times in managed forests.

With so little data and heterogeneous sites, it is hard to draw any overarching conclusions about the relationship of forest characteristics and disturbance quality. At least, it can be said that irrespective of forest type or dominant species, stand-scale disturbances were observed. As old spruce-dominated forests are usually considered prone to frequent/continuous small-scale gap dynamics (Kuuluvainen & Aakala 2011), the spruce forests in this study seemed to have more like clustered medium-severity peaks roughly once in a century. The fire scar data from Polttiais hollow indicated fires in years 1654, 1734, 1914, and 1949 that show very little or not at all in our disturbance data. This could have many explanations, for example that the disturbances seen in the chronology are caused by another agent and the fires dated have been really small scale and not affected our sample plots, or the possible fire before the 1820s has been devastating, leaving few trees to sample. Due to strict fieldwork time, there was no chance to take fire scar samples from Olga hollow. Anyhow, the methods used, unavoidably leave the question of disturbance agent more or less open.

The Pine hollow site had very typical disturbance quality and forest characteristics for a xeric, pine-dominated stand that has been well described in the literature (Gromtsev 2002, Wallenius et al. 2004, Shorohova et al. 2009). The evidence (age structure, fire scar data) from the site suggest a stand with 30-100 year fire interval including high severity disturbances. It is possible that human influence has decreased the amount of older, second or third generation trees due to selective cuttings and increased the frequency of fires.

The most unique site in our data, was the Larix hollow, with four almost equally dominant species, cohort structures and disturbances with varied severity, scale and frequency. The found evidence on fire scars, indicates fires in years 1684, 1734, 1771 and 1919. The fire in 1734 would perfectly fit to the first pulse of disturbance in our chronology. This affected two of the three plots. Also the fire in 1771 could have affected the establishment of pine recruitment to the first plot, although the time span is relatively wide in this case. Considering all the evidence from disturbance chronologies and other field data, it seems that in Larix hollow, there has been one stand scale fire disturbance before the 1740s and smaller, local disturbance, around the turning of the 1800s that affected one plot and during the 1900s, there has been small-scale gap formation and regeneration due to senescence of the dominant tree cohorts.

The forest age structure and disturbance patterns are strongly interlinked and 'mirror' each other seamlessly. High and medium severity disturbances create relatively even-aged cohorts, usually having small proportion of the older generation trees as remnants. In the absence of high severity disturbances, the small-scale senescence and dying of the dominant, canopy layer trees can create periods of continuous recruitment and heterogeneous age structure. Depending on the disturbance frequency, and especially connected with medium or high severity disturbances and shade-intolerant species, there can be long periods without new recruitment, leaving even 100 year long gaps to the age class distribution. These patchy or multimodal age structures in uneven-aged forests are also recognized in the early literature by Dyrenkov (1984, cited in Shorohova et al. 2009).

The use of the Bray-Curtis metric and the Shannon index based disturbance index gives us a useful way to describe, quantify, and compare the disturbance properties of different plots and sites, even with little data. The calculated disturbance index values, settling around the middle of the scale (-1.5), reflect the variability in disturbance frequency and severity. The plots/sites had neither solely clustered (high severity) nor scattered (low severity) decadal disturbances, but they had both.

5 CONCLUSIONS

The disturbance dynamics showed significant variation in spatial and temporal scales between sites and sample plots. During the 22-26 decades of observation, all the sites experienced mixed-severity disturbances from low (0-20%) to moderate (20-40%) or low to high severity (>40%) disturbances. The temporal pattern of disturbances varied between sites and was typically clustered to 1-4 decades, leaving many decades (8-15) with little or no evidence of disturbance. At least three, or possibly all, of the study sites have gone through a stand-scale disturbance during the last three centuries. When comparing the spatiotemporal pattern and synchronicity of disturbances, it seems that there was no synchronization between sites, but the plots in a site were synchronized to some extent. No regional scale disturbances were observed. There was no clear connection between forest characteristics and disturbance quality but our evidence

emphasize the variability of intensity and spatial scale, irrespective of dominant tree species or composition.

The novelty value of this study is in the several centuries long time perspective and evidence from understudied southern boreal forests. The historical insight gives us a better possibility to reflect the changing future conditions and address the important questions for upcoming research. For example, if the past natural disturbance dynamics has been more driven by local conditions and events than regional climate conditions, will this remain with the ongoing climate change? And to what extent, is it possible (or desirable), to preserve the variable natural disturbance dynamics and characteristics of forests along with the diminishing natural forest area and increasing human impact?

Acknowledgements

This study is part of a wider research project called EBOR (Ecological history and long-term dynamics of the boreal forest ecosystem) that aims to unravel the history and disturbance dynamics of Finnish and western Russian forests, in a very long – the last 3000 years – time perspective. EBOR tries to combine study material and data collected from different sources and create new ways to model the impacts of climate, forest fires and human activity on the forest structure and dynamics. The project is funded by Academy of Finland (Suomen Akatemia) and is carried out between years 2014-2018 in cooperation with the faculties of forest sciences, geography and mathematical sciences of Helsinki University.

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APPENDIX 1 Expedition field form

EBOR, Vodlozero expedition Maastolomake, lustokairaukset

Päivämäärä: Kohteen nimi: Koealan nro:

Etäisyys kohteesta: Suunta kohteesta:

Metsätyyppi: Keskipisteen koordinaatit:

Kasvillisuus:

* 1 = Picea abies, 2 = Pinus sylvestris, 3 = Betula pendula, 4 = Betula pubescens, 5 = Betula sp., 6 = Larix sibirica, 7 = Populus tremula, 8 = Sorbus aucuparia 9 = Alnus glutinosa, 10 = Alnus incana

*** Latvuksen suunta + etäisyys neljästä pisteestä

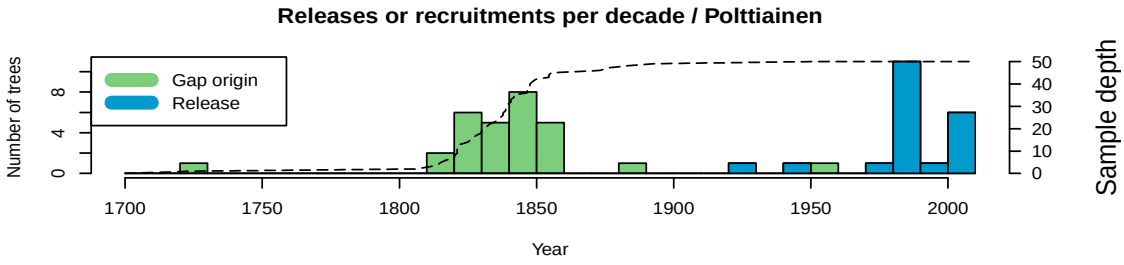
** V = valtapuu, L = lisävaltapuu

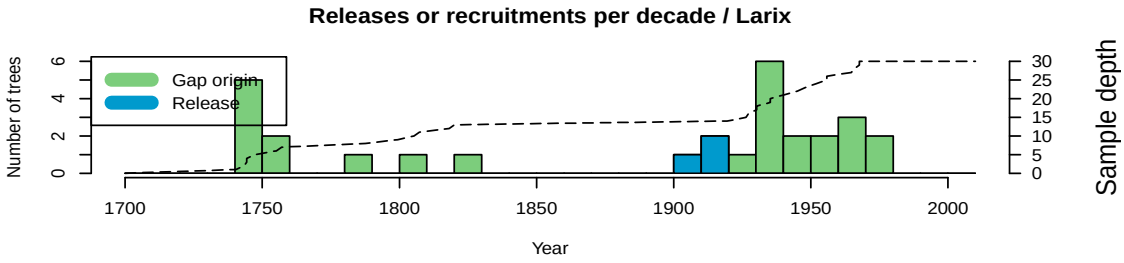
Koealan säde:

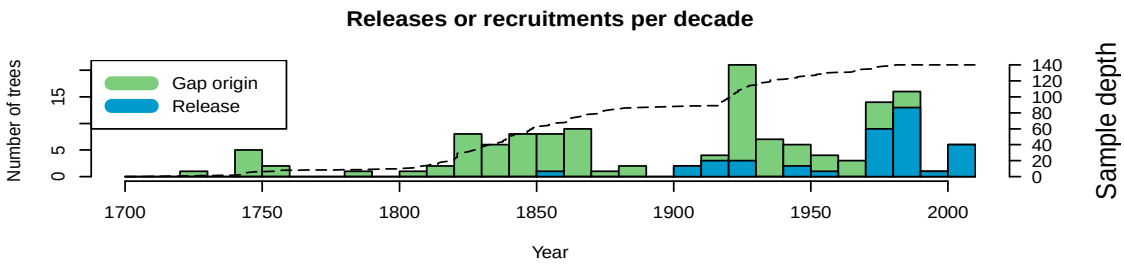
Kuvaus kohteesta/ huomiot:

Koepuu	1	2	3	4	5	6	7	8	9	10	lisä	lisä	lisä
Puulaji*													
DBH (cm)													
Pituus (m)													
Etäisyys kp:stä													
Suunta kp:stä													
Asema latvuksessa**													
PPA Picea													
PPA Pinus													
PPA Larix													
PPA lehti													
Kairauskorkeus (cm)													
Latvus 1 ***													
Latvus 2													
Latvus 3													
Latvus 4													
Latvuksen etäisyys kp:sta													
Latvuksen suunta kp:sta													

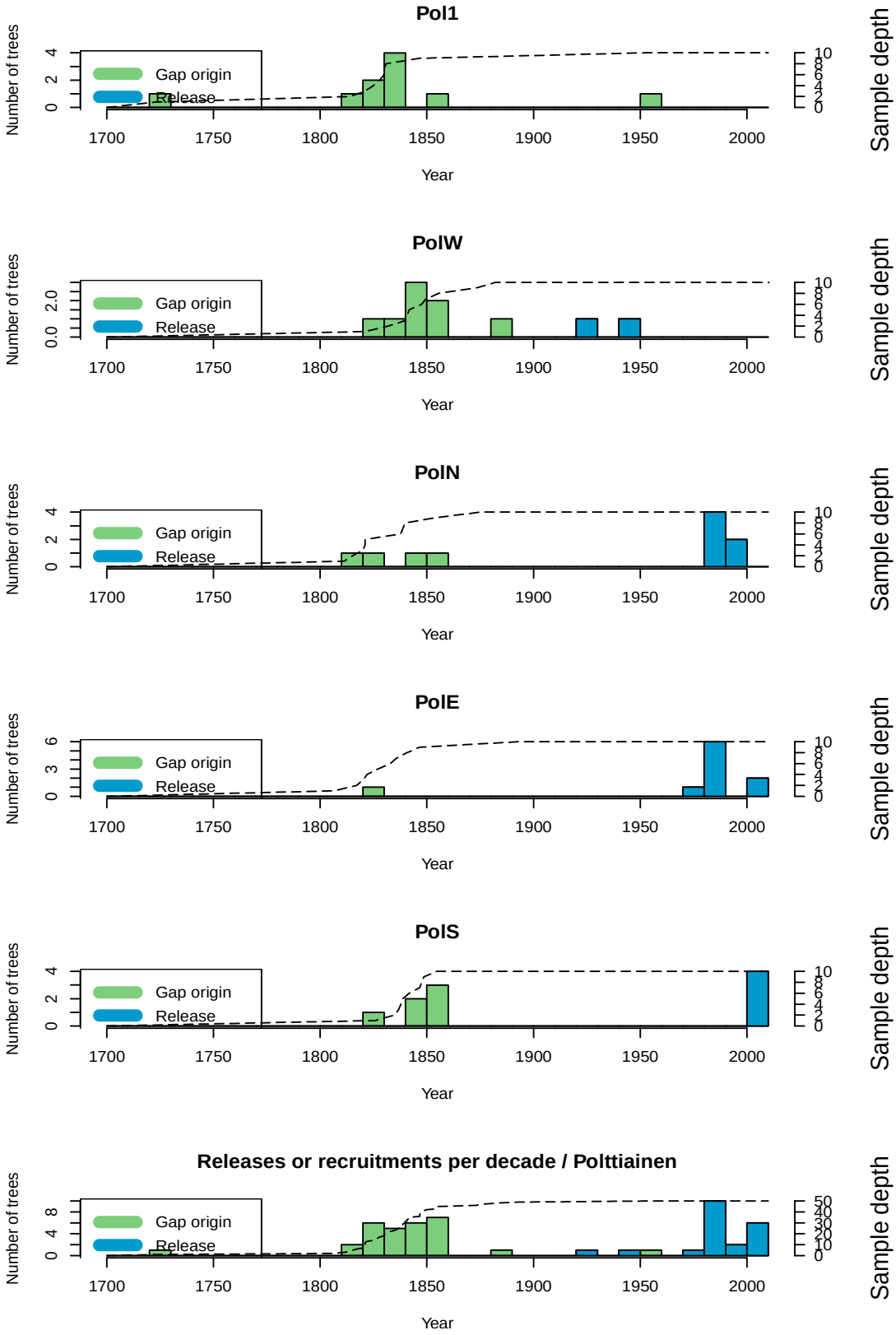
APPENDIX 2 Disturbance chronologies from all sites and plots

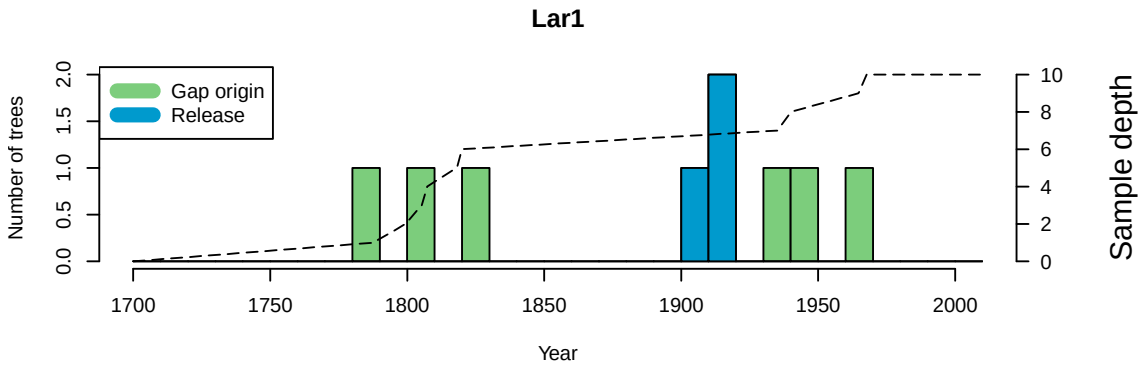






Disturbance chronologies of sites and plots separately




Lar1
Gap origin
Release
Number of trees
Sample depth
Year
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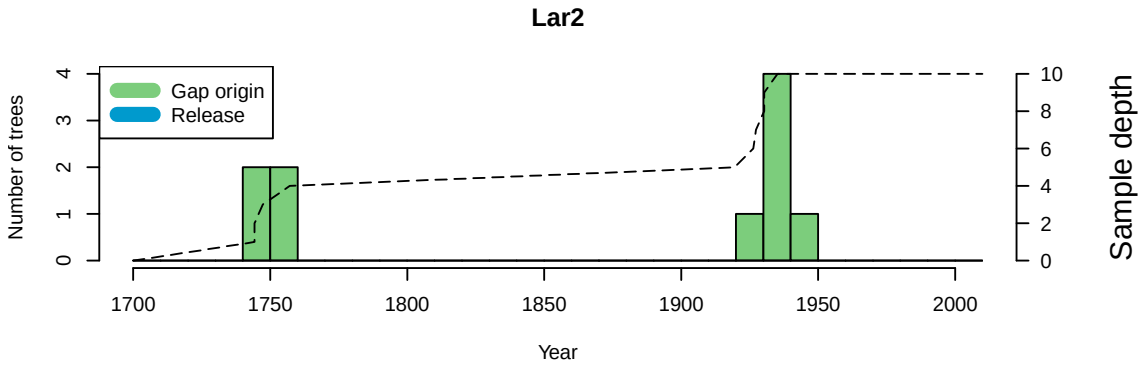
0.5
1.0
1.5
2.0
0
2
4
6
8
10
1700
1750
1800
1850
1900
1950
2000


Lar2
Gap origin
Release
Number of trees
Sample depth
Year
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2
3
4
0
2
4
6
8
10
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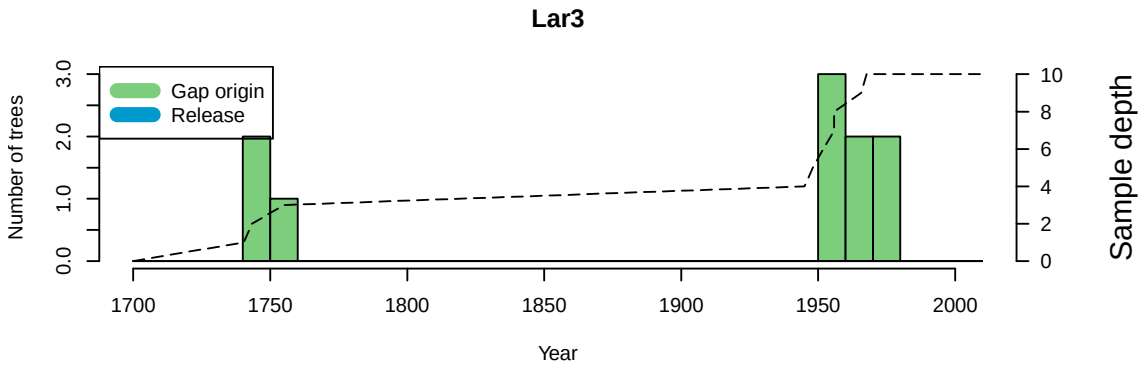
1750
1800
1850
1900
1950
2000


Lar3
Gap origin
Release
Number of trees
Sample depth
Year
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1.0
2.0
3.0
0
2
4
6
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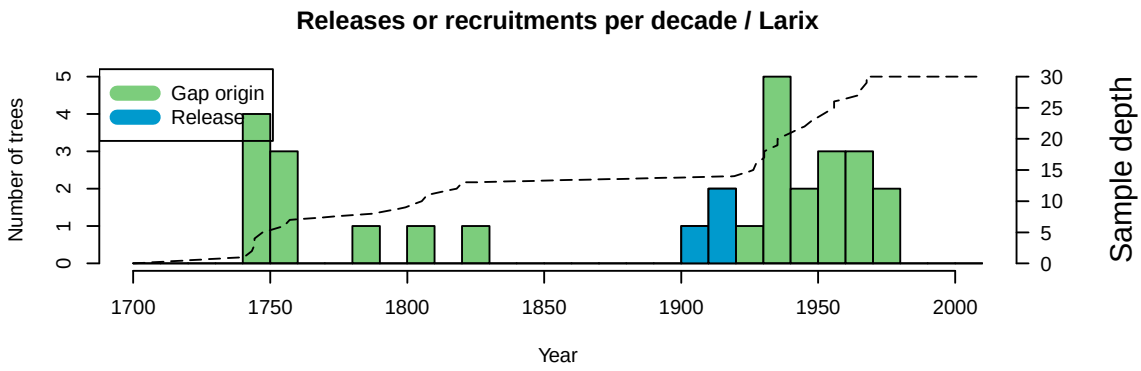
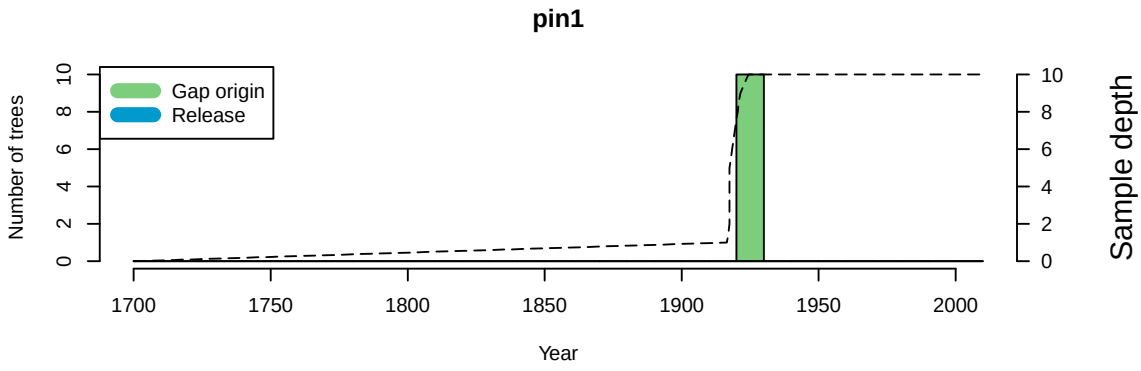
1800
1850
1900
1950
2000


Releases or recruitments per decade / Larix
Gap origin
Release
Number of trees
Sample depth
Year
0
1
2
3
4
5
0
5
10
15
20
25
30
1700
1750
1800
1850
1900
1950
2000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Gap origin
Release
Number of trees
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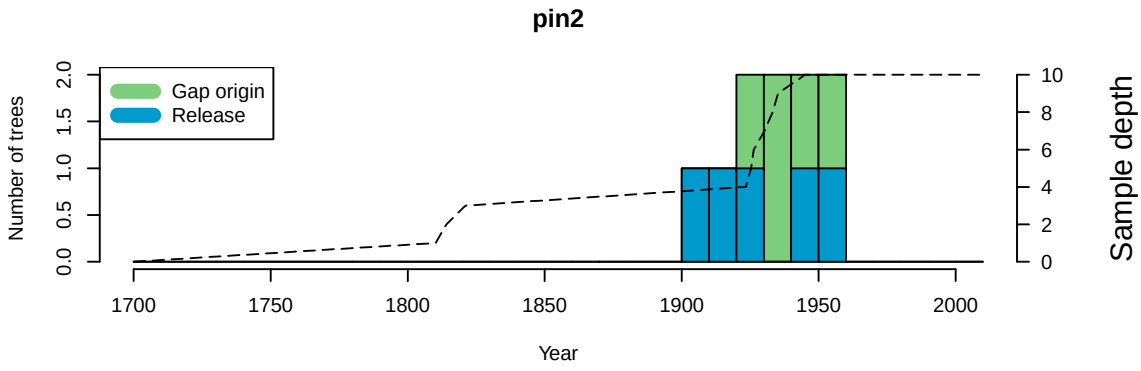
1700 1750 1800 1850 1900 1950 2000
Year
0 2 4 6 8 10
Sample depth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Release
Number of trees
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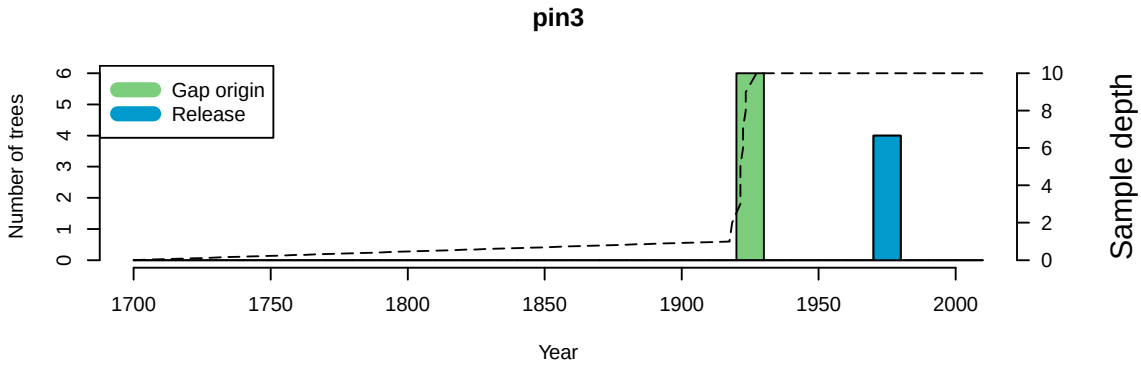
1700 1750 1800 1850 1900 1950 2000
Year
0 2 4 6 8 10
Sample depth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Number of trees
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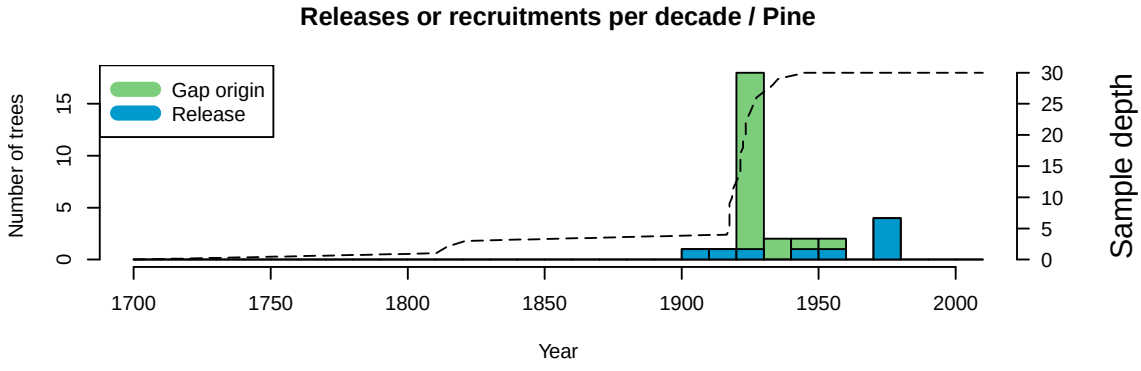
1700 1750 1800 1850 1900 1950 2000
Year
0 2 4 6 8 10
Sample depth


Releases or recruitments per decade / Pine
Gap origin
Release
Number of trees
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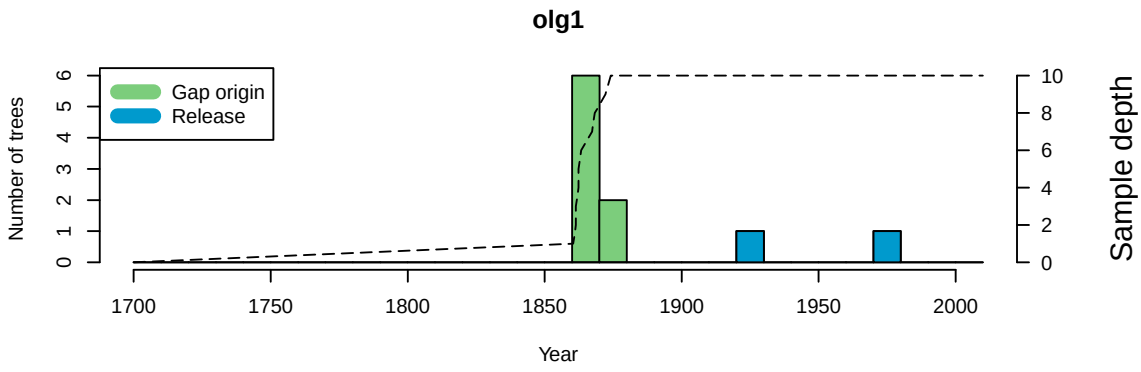
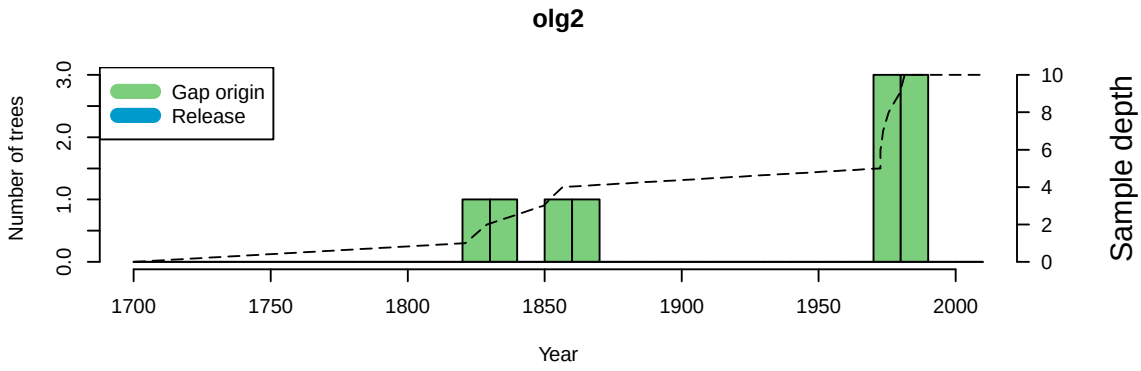
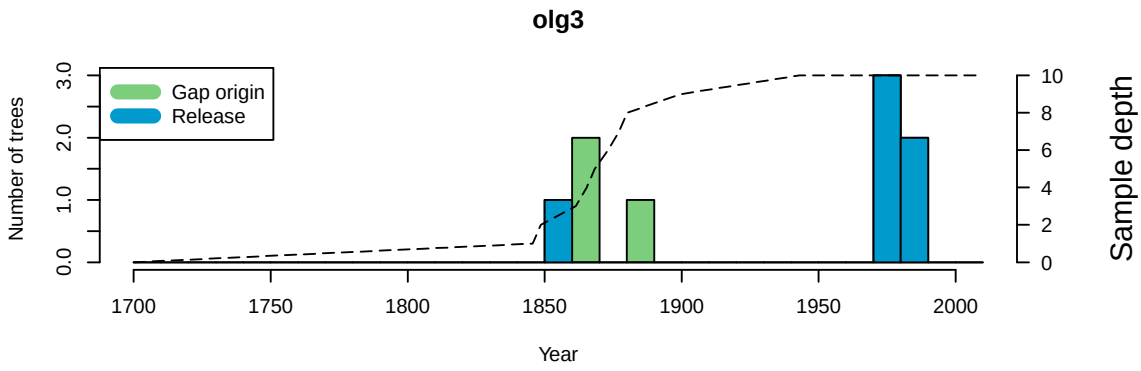
1700 1750 1800 1850 1900 1950 2000
Year
0 5 10 15 20 25 30
Sample depth


olg1
Gap origin
Release
Number of trees
0 1 2 3 4 5 6
1700 1750 1800 1850 1900 1950 2000
Year
0 2 4 6 8 10
Sample depth


olg2
Gap origin
Release
Number of trees
0.0 1.0 2.0 3.0
1700 1750 1800 1850 1900 1950 2000
Year
0 2 4 6 8 10
Sample depth


olg3
Gap origin
Release
Number of trees
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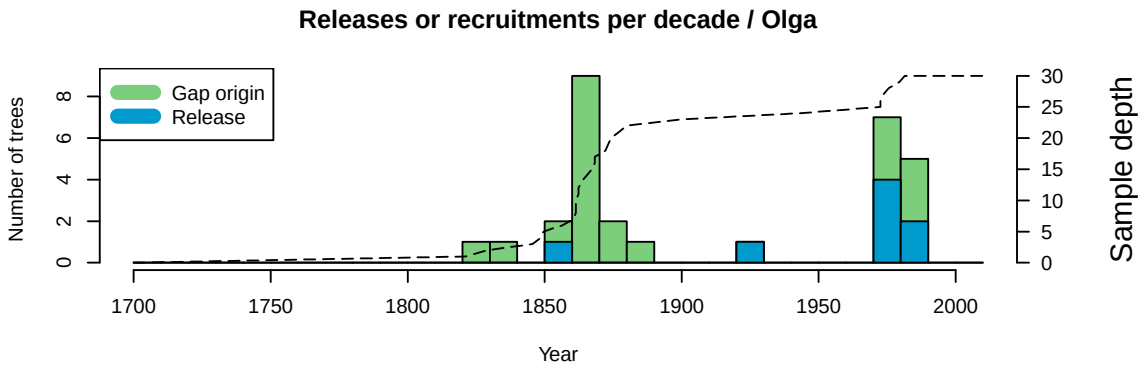
1700 1750 1800 1850 1900 1950 2000
Year
0 2 4 6 8 10
Sample depth


Releases or recruitments per decade / Olga
Gap origin
Release
Number of trees
0 2 4 6 8
1700 1750 1800 1850 1900 1950 2000
Year
0 5 10 15 20 25 30
Sample depth

APPENDIX 3 Disturbance index (DI) and Bray-Curtis dissimilarity metric (BC) results

BC	Pol	Olg	Pin	Lar
Polttianen	0	0.7657867	0.9416292	0.9058475
Olga	0.7657867	0	0.8678875	0.9323919
Pine	0.9416292	0.8678875	0	0.7527033
Larix	0.9058475	0.9323919	0.7527033	0

DI	plot 1	plot 2	plot 3	plot 4	plot 5
Polttiainen	-1.326094	-1.75918	-1.3680907	-1.159737	-1.25088
Olga	-1.120741	-1.279066	-0.9509772	*NA*	*NA*
Pine	0	-1.693464	-0.68036	*NA*	*NA*
Larix	-1.742321	-1.400808	-1.4861559	*NA*	*NA*